

Neurocognitive and Neurophysiological Correlates of Motor Planning During Familiar and Novel Contexts

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Objective: Research suggests that behavioral indices of motor planning (i.e., latencies that precede motor output) (a) relate to processing speed (PS) and executive functioning (EF), but not working memory (WM), and (b) deteriorate in novel contexts. It is not clear whether an electrophysiological index of motor planning (i.e., movement-related cortical potentials; MRCPs) also relates to PS and EF, and whether it deteriorates in novel contexts. This study sought to clarify associations among these variables while manipulating contextual novelty. **Method:** Forty healthy adults completed standardized measures of PS, EF, and WM. Participants performed highly familiar motor sequences in familiar versus novel contexts during EEG recording, while motor planning latencies and peak MRCPs were obtained. Hierarchical regressions assessed the relative contributions of PS, EF, and WM to motor planning latencies and MRCPs. **Results:** Novel contexts elicited longer planning latencies ($g_{av} = 1.96$) and reduced MRCPs ($g_{av} = .24$) compared to familiar contexts. PS predicted planning times in both familiar ($R^2 = .12$) and novel contexts ($R^2 = .15$), while EF contributed additional variance during novel contexts only (R^2 Change = $.10$). EF was the sole predictor of MRCPs in both familiar ($R^2 = .12$) and novel contexts ($R^2 = .18$). WM did not predict planning latencies or MRCPs. **Conclusions:** Contextual novelty alone can decrease performance and neural activation during complex sequencing. The general link between preparatory activation and EF suggests that capacity limitations drive novelty effects, and implies a common substrate underlying motor planning and higher-order behavioral control.

Keywords: action planning, executive functioning, motor sequencing, movement-related cortical potentials, novelty

Motor (or action) planning refers to covert generation of internal models or plans for action. These plans are thought to implicitly take into account both the overall movement goals and the specific muscular commands (Buxbaum, Johnson-Frey, & Bartlett-Williams, 2005; Keele, 1968; Wolpert, 1997), an idea that is supported by the distinct effects of cognitive versus physical task demands on different phases of preparatory neural activity (Shibasaki & Hallett, 2006). From a neuroanatomic standpoint, motor planning is thought to originate in bilateral supplementary motor regions, including the supplementary motor area proper (SMA), as well as pre-SMA and the cingulate motor area (Cunnington, Windischberger, & Moser, 2005; Ikeda & Shibasaki, 2003). Other evidence for the association between SMA and motor planning comes from clinical studies that demonstrate either reduced spon-

taneous movement following SMA lesions (e.g., akinetic mutism, Bannur & Rajshekhar, 2000; Hanlon, Clontz, Snow, & Thomas, 1995; Krainik et al., 2001; Nagaratnam, Nagaratnam, Ng, & Diu, 2004), or impaired inhibition of purposeful movements following lesions to SMA and surrounding structures (Feinberg, Schindler, Flanagan, & Haber, 1992; Giovannetti, Buxbaum, Biran, & Chatterjee, 2005; Nachev, Kennard, & Husain, 2008). Additionally, functional MRI research has demonstrated an association between the efficiency of motor planning and the connectivity strength between the SMA and the basal ganglia (Marchand et al., 2013), suggesting that motor planning may represent an index of the SMA integrity. Lastly, electrophysiological (EEG) research shows that motor planning is associated with movement-related cortical potentials (MRCPs; Jahanshahi & Hallett, 2003a), which are low-frequency, negative voltage event-related potentials that precede the onset of voluntary and cued movements (Brunia, van Boxtel, & Böcker, 2011; Deecke, Scheid, & Kornhuber, 1969). Within the MRCP literature, it is well established that the early readiness potential that precedes self-paced movements is maximal over fronto-central scalp electrodes, reflecting, at least in part, contributions from SMA and related structures (Gerloff, 2003).

From a behavioral standpoint, the process of motor planning is reflected in brief latencies that occur just prior to the initiation of motor output (Bortoletto & Cunnington, 2010; Klimkeit, Mattingley, Sheppard, Lee, & Bradshaw, 2005; Romero, Van Gemmert, Adler, Bekkering, & Stelmach, 2003). Past research has shown that the length of the motor planning latencies (MPLs) depends on the characteristics of the planned actions, such that MPLs increase

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with the increasing complexity (or length) of the planned motor sequence (Grootens et al., 2009; Suchy & Kraybill, 2007), and decrease as the sequence becomes more familiar (Gidley Larson & Suchy, 2014b). Additionally, there appear to be individual differences in MPLs, such that latencies increase as a function of normal aging (Berchicci, Lucci, Pesce, Spinelli, & Di Russo, 2012; Suchy & Kraybill, 2007). Lastly, MPLs appear to depend on situational factors, such that latencies increase when a motor sequence is performed in a novel context (Gidley Larson & Suchy, 2014b; Suchy & Kraybill, 2007). Interestingly, exaggerated increases in MPLs in novel contexts have been shown to be uniquely sensitive to subtle subclinical cognitive changes associated with incipient cognitive decline in old age (Suchy, Kraybill, & Franchow, 2011), as well as subclinical consequences of mild traumatic brain injury (Suchy, Euler, & Eastvold, 2014), either of which were not detectable with traditional clinical measures of neurocognitive integrity.

Although the neurocognitive underpinnings of motor planning have not been extensively studied, research to date suggests that MPLs correlate with general psychomotor speed (Suchy & Kraybill, 2007), as well as with the overall speed of subsequent motor output (Gidley Larson & Suchy, 2014b; Marchand et al., 2013). In contrast, MPLs do not seem to notably benefit from verbal rehearsal of the planned action, suggesting that working memory may not contribute to motor planning (Gidley Larson & Suchy, 2014b). Importantly, despite the apparent lack of association between MPL and working memory, there is evidence that MPLs are associated with executive functioning (i.e., the abilities to plan, organize, and successfully execute mental and behavioral actions), even after controlling for psychomotor speed and age (Kraybill & Suchy, 2008; Suchy & Kraybill, 2007; Suchy, Kraybill, & Gidley Larson, 2010). In fact, in combination with other indices of performance on a motor sequencing task, MPLs have outperformed traditional measures of executive functioning in estimating instrumental activities of daily living in older adults, both concurrently and at a one year follow-up (Kraybill & Suchy, 2011; Kraybill, Thorgusen, & Suchy, 2013), once again pointing to the potential clinical utility of the construct of motor planning in neuropsychological evaluations.

In sum, past research suggests that (a) MPLs, while related to psychomotor speed, may also represent a sensitive index of executive functioning above and beyond speed and separate from working memory, and (b) increases in MPLs in *novel contexts* may be particularly sensitive to subtle, subclinical neurocognitive changes that cannot be detected with traditional neuropsychological measures. For these reasons, better understanding of the construct of motor planning, under both familiar and novel conditions, is warranted. The purpose of the present study is to examine neurocognitive correlates of both neural (i.e., MRCPs) and behavioral (i.e., MPLs) indices of motor planning, under both novel and familiar contexts, while addressing the following limitations of past research.

First, while past research has demonstrated the association between executive functioning and motor planning, this research is confounded by the fact that MPLs were measured while participants were also learning new motor sequences. Given that it is generally assumed that executive functioning becomes invoked under novel circumstances, it is not clear from past research whether executive functioning relates to motor planning in general,

or rather only motor planning during the learning process. To address this limitation, the present study examines the association between executive functioning and MPLs for sequences that are highly familiar to the participants.

Second, in a related vein, while past research has shown that MPLs increase under novel contexts, these findings are once again confounded by the fact that the participants were also learning new sequences when MPLs were assessed (Kraybill & Suchy, 2008, 2011; Kraybill et al., 2013; Suchy & Kraybill, 2007; Suchy et al., 2010). Although in one study the effect of novel context was demonstrated even when the sequences had been overlearned (Gidley Larson & Suchy, 2014b), in this study only a single instance of a novel context occurred, making it unclear whether any one aspect of the novel context could have affected the results. To address these limitations, this study examines the impact of novel context on MPLs that precede highly familiar and overlearned motor sequences, and introduces a high number of different novel contexts to avoid the possibility that one particular contextual characteristic is responsible for the findings.

Third, while it is assumed that MRCPs relate to motor planning, it is not clear whether they have the same neurocognitive correlates as MPLs do. Although much is known about the effects of particular experimental manipulations (Shibasaki & Hallett, 2006) and clinical conditions on readiness potential amplitudes (Gerloff, 2003; Praamstra, Jahanshahi, & Rothwell, 2003; Westphal, 2003), we are aware of no prior studies that have examined the broader neurocognitive correlates of movement-related potentials in healthy individuals. Moreover, relatively few studies of MRCPs have examined preparatory neural activity while participants performed complex praxis movements (though see Wheaton, Fridman, Bohlhalter, Vorbach, & Hallett, 2009; Wheaton, Shibasaki, & Hallett, 2005), thereby limiting their generalization to the neuropsychological literature on complex motor sequencing. Thus, by investigating the neurocognitive correlates of both neural and behavioral motor planning indices, the present study can clarify the task features that are most critical to novel context effects, while also exploring dynamic neural mechanisms that may account for those relations.

In sum, the present study examines the neurocognitive correlates of MPLs and MRCPs that were simultaneously recorded from healthy individuals during complex motor sequencing. By using highly practiced sequences together with unexpectedly and frequently changing contexts, the study was designed to isolate the neurocognitive correlates of behavioral and neural motor planning in both familiar and novel contexts, apart from possible contributions due to learning. Importantly, apart from those modifications, the EEG analogue task used in this study was designed to be otherwise faithful to the validated neuropsychological task on which it was based, thus enhancing the generalizability of the overall study findings. In line with previous research, we hypothesized that only psychomotor speed would contribute to variation in MPLs in general (i.e., during familiar contexts), and that executive functions would contribute additional unique variance to MPLs following novel contexts. We predicted no contribution from working memory in either context. Given the lack of prior literature on neurocognitive correlates of MRCPs, we expected to observe the same pattern for MRCP amplitudes.

Method

Participants

Forty-seven undergraduate volunteers enrolled in psychology courses at the University of Utah participated in the study in exchange for course credit. All participants were right-handed, had normal or corrected-to-normal vision, normal color vision, and reported no history of neurological or psychiatric disorders. Seven participants were excluded from data analysis for the following reasons: technical failure during data collection ($n = 3$), problems complying with task demands (indicated by correct performance on fewer than 5 vigilance trials; $n = 2$), excessive EEG artifacts from muscle movements ($n = 1$), or MRCP amplitude greater than 3.5 SD above the sample mean ($n = 1$). The final sample used in analyses consisted of 40 undergraduate students who were mostly female (65%) and had a mean age of 26.28 ($SD = 8.64$, Range = 18–52).

Experimental Procedures and Instruments

Informed consent was obtained from all participants and the university's Institutional Review Board approved all procedures. As part of a larger study, participants completed a 90-min battery of traditional neuropsychological tests, including measures designed to assess

psychomotor speed, working memory, and executive functioning. Following completion of the battery, participants completed an electronically administered complex motor sequencing task while EEG activity was recorded. Descriptive statistics for the independent and dependent variables are listed in Table 1.

Executive Functioning

Executive functioning was assessed using Trail Making Test (Letter Number Sequencing Condition completion time), Design Fluency (total correct designs completed across all conditions), and Verbal Fluency (total words generated across all conditions) subtests from the Delis-Kaplan Executive Function System (D-KEFS; Delis, Kaplan, & Kramer, 2001), and the Color-Word page from the Stroop Color and Word test (Golden & Freshwater, 1998). We converted raw scores to z scores and computed a mean z score across all four tests; consistent with prior research in this area (Kraybill & Suchy, 2011; Kraybill et al., 2013). Cronbach's alpha for this composite in this sample was .791.

Psychomotor Speed

To assess psychomotor speed, we used tasks designed to control for component processes of the executive tests used in this study.

Table 1
Descriptive Statistics for Neurocognitive Variables, Motor Planning Latencies, and Movement-Related Cortical Potentials

| Variable | Range | M (SD) |
|--------------------------------------|--------------|-------------------|
| Psychomotor speed | | |
| Stroop word | 70–131 | 101.53 (15.72) |
| Stroop color | 50–103 | 76.35 (12.05) |
| Trails visual scanning (s) | 11–23.04 | 16.19 (2.84) |
| Trails letter sequencing (s) | 11.93–43 | 23.32 (7.41) |
| Psychomotor speed composite | –2.21–1.62 | 0 (.76) |
| Working memory | | |
| Digit span forward | 6–16 | 10.40 (2.41) |
| Digit span back | 5–15 | 8.78 (2.46) |
| Arithmetic | 8–21 | 14.30 (3.15) |
| Working memory composite | –1.44–1.80 | 0 (.74) |
| Executive functioning | | |
| Letter fluency | 22–70 | 41.82 (10.67) |
| Category fluency | 24–68 | 43.50 (9.08) |
| Category switching | 10–22 | 15.15 (2.60) |
| Design fluency filled | 6–21 | 13.70 (3.96) |
| Design fluency empty | 8–21 | 14.15 (3.55) |
| Design fluency switching | 4–18 | 9.75 (2.65) |
| Trails letter-number sequencing (s) | 32.44–139.50 | 62.13 (22.14) |
| Stroop color word | 32–65 | 48.05 (8.77) |
| Executive composite | –1.18–1.39 | 0 (.64) |
| Planning times | | |
| Novel context planning times (ms) | 681.75–1,923 | 1,248.46 (235.02) |
| Familiar context planning times (ms) | 507–1,223.85 | 845.07 (173.22) |
| Accuracy | | |
| Novel context errors | 3–45 | 16.32 (9.73) |
| Familiar context errors | 1–36 | 13.73 (8.60) |
| MRCPs | | |
| Novel contexts (mV) | –6.67–-.21 | –3.19 (1.76) |
| Familiar contexts (mV) | –7.26–-.25 | –3.62 (1.76) |

Note. All neurocognitive variables reflect raw total correct except where completion time is indicated in s. Composite scores are in standardized units. Accuracy values reflect the number of errors committed out of a possible 100 trials administered in each condition. MRCPs = movement-related cortical potentials; mV = microvolts.

Specifically, we used the visual scanning and letter sequencing conditions on the Trail Making Test from the D-KEFS battery (Delis et al., 2001) and the color and word pages from the Stroop Color and Word test (Golden & Freshwater, 1998). Participants' raw scores were converted to z scores and combined into a single composite that was used for the principle analyses. Cronbach's alpha for this composite in this sample was .610.

Working Memory

To assess working memory ability we administered the Working Memory subtests of the Wechsler Adult Intelligence Scale, 4th edition (Wechsler, 2008). Specifically the subtests included in the composite were: Digit Span Forward, Digit Span Backward, and Arithmetic. Cronbach's alpha for this composite in this sample was .594.

Motor Sequencing Task

The motor sequencing task used in this study was based on the Push-Turn-Tap (PTT) task (Suchy & Kraybill, 2007) from the Behavioral Dyscontrol Scale–Electronic Version (Suchy, Derbidge, & Cope, 2005), which is an electronic analogue of Alexander Luria's fist edge palm task (Luria, 1966). Participants performed this task during EEG recording. Stimuli were presented using Presentation software (version 16.3, Neurobehavioral Systems). Each trial of the task involved the presentation of a black fixation cross on a gray screen for 1,000 milliseconds, followed by a slide presenting the familiar four-movement sequence, which was a combination of the movements push, turn, and tap-tap. Push (P) required the participant to push a joystick on the response console toward the screen in front of them, turn (T) required them to turn the joystick clockwise, and tap-tap (tt) required them to tap twice on a white dome on the response console (see Figure 1). Participants were instructed that the sequence could change on any trial so they would need to pay close attention to each screen to ensure they performed each sequence correctly. Participants were asked to respond as quickly as possible following presentation of

each sequence while also being careful to perform the movements precisely.

To ensure that results could not be explained by the idiosyncrasies of any one given sequence, each participant was randomly assigned one of 10 different sequences (with which he or she then became familiar), all of which began with either push or turn. Additional constraints on the sequences included that tap-tap appear only once, and no movement was repeated in adjacent positions during the sequence (aside from tap-tap; e.g., PTtT, PttTP, TPttT, etc.). A randomly varying intertrial interval of 1,000–3,000 ms followed each trial, during which a blank gray screen was displayed. Any errors made by participants were indicated by a ding and were followed by the automatic initiation of the next trial. To ensure that participants were familiar with the task and their familiar sequence, 20 practice trials were included at the start of the task. Participants then completed a total of 500 trials and were given the opportunity to rest every 50 trials.

Contextual novelty was manipulated pseudorandomly by varying the visual context of the familiar sequence on 20% of trials. Different dimensions of contextual novelty were systematically varied across each of 10 blocks of 50 trials, where each novel context within a block changed one or more visual attributes such as: the printed font of the sequence, the location of the sequence on the screen, the color and or texture of the background, and the inclusion of distracting text and/or objects (see Figure 2). Each novel context trial was followed by at least three repetitions of the same visual context. In all analyses the familiar context condition refers to third repetition of visual context of the familiar sequence (trials representing a fourth repetition were too infrequent to permit valid analyses). In addition to contextual novelty, we also varied the order of the movements in the familiar sequence pseudorandomly on 10% of trials, for the purpose of requiring participants to attend to all sequence presentations. The preceding visual context was always maintained for novel sequence trials (see Figure 3).

In sum, unbeknownst to participants, within each group of five trials the exact number of successively repeated sequences and the relative position in which novel contexts or possible novel sequences were presented was varied pseudorandomly within larger runs of 10 trials and blocks of 50 trials. Altogether, these manipulations were implemented to minimize possible expectancy effects regarding presentation of novel contexts and sequences, and to help ensure that participants stayed alert and engaged throughout the task.

EEG Recording

Participants were seated in a sound- and light-attenuated room during EEG acquisition. EEG signals were sampled online at 1,024 Hz using a 64-channel Ag/AgCl electrode WaveGuard EEG Cap (Advanced Neurotechnology, ANT), and digitalized and recorded using an ANT 64 channel amplifier (ANT Company). Electrode impedances were maintained below 25 k Ω . Additional electrodes were placed at the outer canthi of both eyes and above and below the right eye to monitor blinks and other eye movements.

EEG Preprocessing

EEG data were preprocessed using the ASA-lab software package (version 4.7.12 ANT Neuro, Enschede, The Netherlands), as



Figure 1. Response console used for the complex motor sequencing task. Arrows depict the movements comprising the sequences. See the online article for the color version of this figure.

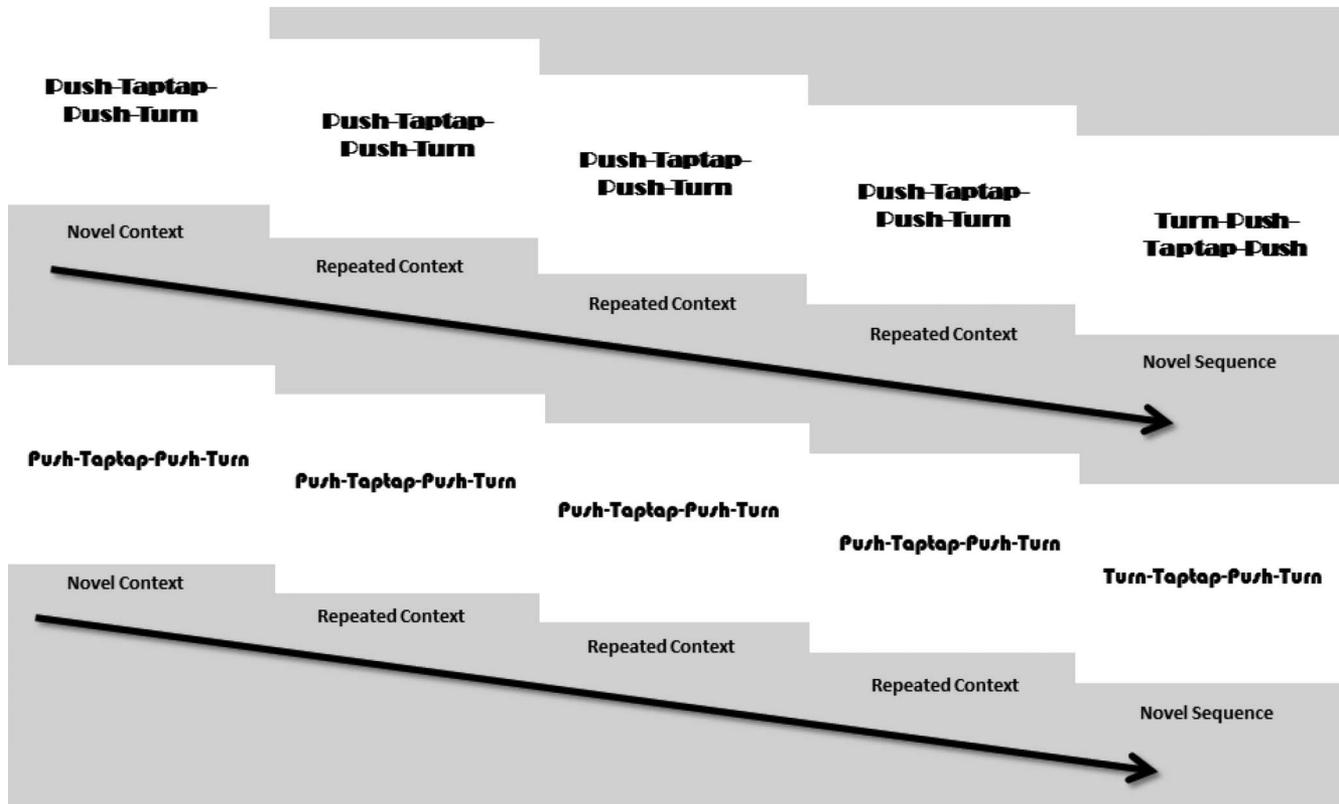


Figure 3. Example run of 10 trials depicting a representative order of novel context and novel sequence presentations. Within each run of 10 trials a novel context was always presented on Trial 1, and 5, 6, or 7. Novel sequences provided a vigilance check and were presented half as often on Trial 5, 9, or 10. In all cases three or four repeated contexts followed every novel context with no intervening novel stimuli.

committed significantly more errors in response to novel versus familiar contexts $t(39) = 3.43, p = .001, 95\% \text{ CI } [1.07, 4.13]$, Hedge's $g_{av} = 0.28$, further indicating the efficacy of the manipulation (and see accuracy statistics in Table 1). Effect sizes indicated by Hedge's g_{av} were calculated using the supplementary algorithms provided by Lakens (2013).

Principal Analyses

Due to the expected intercorrelations among the neurocognitive variables, we conducted a series of hierarchical regressions, examining the relative contributions of each predictor to the four dependent variables. Specifically, we conducted four analyses, using MRCP and MPLs under novel and familiar context as the dependent variables, and the three neurocognitive variables of interest (EF, PS, and WM) as predictors. In line with the hierarchical structure of cognition that states that lower order processes (i.e., PS) represent a necessary component process for EF performance, for each analysis we entered PS on Step 1. Next, in line with the conceptualization of WM as the mental control (as opposed to behavioral control) component of EF (McCabe et al., 2010), WM was entered on Step 2. Lastly, EF was entered on Step 3. In this manner, we accounted for component processes of EF, allowing us to determine whether purely executive/behavioral con-

trol abilities contributed to motor planning above and beyond the other variables.

As seen in Tables 3 and 4, using MRCP-familiar and MRCP-novel as the dependent variables yielded EF as the only significant predictor, above and beyond PS and WM. Importantly, EF accounted for approximately 12% and 18% of variance, respectively, which is considerable given that there is no method variance overlap between MRCP and behaviorally assessed EF. Of note, reversal of the order of variable entry on Steps 1 and 2 (i.e., entering WM first and PS second) did not alter the results (i.e., WM did not emerge as a significant predictor even when entered first).

As seen in Tables 5 and 6, using MPL-familiar and MPL-novel as the dependent variables yielded PS as significant predictor, accounting for approximately 12% and 15% of variance, respectively. In addition, in the novel context condition, EF also emerged as a significant predictor, accounting for an additional 10% of variance. Once again, reversing the order of variable entry on Steps 1 and 2 (i.e., entering WM first and PS second) did not alter the results (i.e., WM did not emerge as a significant predictor even when entered first).

Taken together, these findings demonstrate that (a) EF represents the sole predictor of MRCP, regardless of context, (b) PS represents the sole predictor of MPLs in familiar contexts, and (c) both PS and EF contribute variance to MPLs in novel contexts.

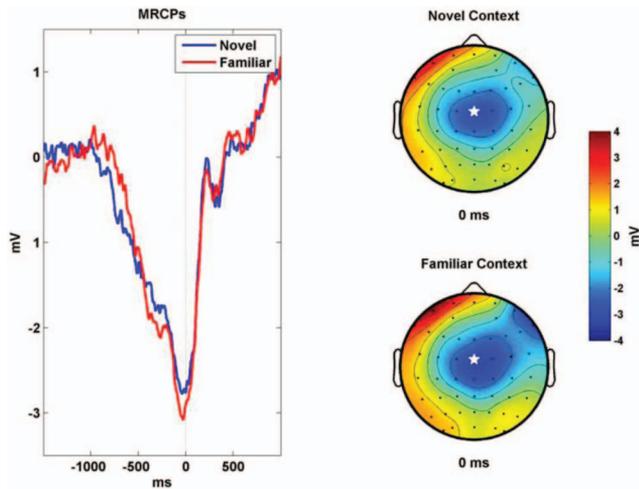


Figure 4. Left: Grand-averaged movement-related cortical potentials elicited in response to novel and familiar contexts, time-locked to the initiation of participants' first movement in the sequence. Right: Grand-averaged scalp topography demonstrating a maximal negativity at electrode FCz (white stars) time-locked to participants' first movement in both conditions. See the online article for the color version of this figure.

WM does not appear related to either the neural or the behavioral indices of motor planning, regardless of context.

Discussion

Prior research on complex sequencing has typically measured novelty effects under conditions where participants were also simultaneously learning new sequences. To clarify the contribution of sequence learning versus novelty per se, the present EEG analogue task used highly familiar sequences and only manipulated contextual novelty (with sequence novelty only acting to ensure good task compliance). By combining these methodological controls with simultaneous EEG recording, the present study was able to isolate the neurocognitive correlates of both behavioral and electrophysiological indices of motor planning.

Table 2
Zero-Order Correlations Among Motor Planning Latencies, Movement-Related Cortical Potentials, and Neurocognitive Variables

| | MRCP-F | MPL-N | MPL-F | EF | PS | WM |
|--------|--------|-------|-------|--------|-------|-------|
| MRCP-N | .89** | .32* | .29 | -.44** | -.21 | -.05 |
| MRCP-F | | .24 | .32* | -.38* | -.20 | -.02 |
| MPL-N | | | .76** | -.48** | -.39* | -.17 |
| MPL-F | | | | -.37* | -.35* | -.19 |
| EF | | | | | .59** | .42** |
| PS | | | | | | .28 |

Note. MRCP-N = movement-related cortical potentials–novel context in microvolts; MRCP-F = movement-related cortical potentials–familiar context in microvolts; MPL-N = motor planning latencies–novel context in milliseconds; MPL-F = motor planning latencies–familiar context in milliseconds; EF = executive functioning composite; PS = psychomotor speed composite; WM = working memory composite.
* $p < .05$ (two-tailed). ** $p < .01$ (two-tailed).

Table 3
Hierarchical Linear Regression Predicting Movement-Related Cortical Potential Amplitudes in Familiar Contexts

| Step | Variable | R^2 | ΔR^2 | ΔF | df | p |
|------|----------|-------|--------------|------------|------|-----|
| 1 | PS | .04 | .04 | 1.62 | 1,38 | .21 |
| 2 | WM | .04 | .00 | .05 | 1,37 | .83 |
| 3 | EF | .17 | .12 | 5.33 | 1,36 | .03 |

Note. df = degrees of freedom; PS = psychomotor speed composite; WM = working memory composite; EF = executive functioning composite.

With regard to the neurocognitive correlates of motor planning latencies (MPLs), the present results clarify several prior findings. First, because the study examined effects of novel contexts completely independent from demands on motor learning, the results suggest that novelty alone is sufficient to elicit performance costs in MPLs, and that those effects are not attributable to idiosyncratic features of particular novel stimuli. On the other hand, results did not demonstrate a general association between executive functioning (EF) and MPLs. Rather, only psychomotor speed (PS) contributed significant variance to motor planning in familiar contexts, whereas EF made additional contributions only in novel contexts. Working memory (WM) contributed no meaningful variance in either context. While the WM findings are consistent with predictions based on prior research (Gidley Larson & Suchy, 2014a), results for EF were in contrast to prior findings that had suggested a strong relation between MPLs and executive functioning in general (Suchy & Kraybill, 2007; Suchy et al., 2010), thus refining the previous understanding. In particular, whereas psychomotor speed supports efficient motor planning in general (i.e., when contexts are stable) executive abilities only appear to be implicated when responding requires overcoming changing environmental demands.

In contrast to the findings for planning latencies, results indicated that EF was the only neurocognitive variable that contributed significant variance to MRCPs in both familiar and novel contexts (12% and 18%, respectively). Thus, higher EF was consistently associated with greater preparatory neural activation during complex sequencing, while psychomotor speed and working memory made no demonstrable contributions. Interestingly, results further indicated that novel contexts actually elicited slightly smaller peak amplitudes compared to familiar contexts. At first glance this may appear counterintuitive, in that if higher EF predicts greater activation across people, and responding to novel contexts is more executively demanding, one might expect the more demanding condition to elicit greater activation across conditions. Neverthe-

Table 4
Hierarchical Linear Regression Predicting Movement-Related Cortical Potential Amplitudes in Novel Contexts

| Step | Variable | R^2 | ΔR^2 | ΔF | df | p |
|------|----------|-------|--------------|------------|------|-----|
| 1 | PS | .04 | .04 | 1.68 | 1,38 | .20 |
| 2 | WM | .04 | .00 | .00 | 1,37 | .95 |
| 3 | EF | .22 | .18 | 8.03 | 1,36 | .01 |

Note. df = degrees of freedom; PS = psychomotor speed composite; WM = working memory composite; EF = executive functioning composite.

Table 5
Hierarchical Linear Regression Predicting Motor Planning Latencies in Familiar Contexts

| Step | Variable | R^2 | ΔR^2 | ΔF | df | p |
|------|----------|-------|--------------|------------|------|-----|
| 1 | PS | .12 | .12 | 5.39 | 1,38 | .03 |
| 2 | WM | .13 | .01 | .37 | 1,37 | .55 |
| 3 | EF | .17 | .03 | 1.45 | 1,36 | .24 |

Note. df = degrees of freedom; PS = psychomotor speed composite; WM = working memory composite; EF = executive functioning composite.

less, this pattern is consistent with other research that has demonstrated reduced preparatory neural activity in conditions of high versus lower cognitive demand (Baker et al., 2011), as well as in clinical conditions associated with motor and/or executive dysfunction (Golob & Starr, 2000; Praamstra et al., 2003; Seo, Sartory, Kis, Scherbaum, & Müller, 2013). At the same time, literature on healthy aging has generally demonstrated the opposite pattern of results, with older adults often exhibiting larger MRCP amplitudes relative to younger individuals (Berchicci et al., 2012; Falkenstein, Yordanova, & Kolev, 2006; Yordanova, Kolev, Hohnsbein, & Falkenstein, 2004), possibly reflecting compensatory processes or dedifferentiation of previously independent substrates (Park & Reuter-Lorenz, 2009; Seidler et al., 2010).

Given the diversity of the MRCP literature that includes studies of single movements (Baker et al., 2011) and complex sequences (Bortoletto & Cunnington, 2010), block (Yordanova et al., 2004) and event-related designs (Hughes, Schütz-Bosbach, & Waszak, 2011), and various between and within-group comparisons (Berchicci et al., 2012), it is beyond the scope of the present study to reconcile these apparent discrepancies. Nevertheless, the present results can be readily integrated by considering the overall pattern of the obtained within- and between-subjects effects. Specifically, novel contexts elicited slightly reduced preparatory activation relative to familiar contexts within individuals, whereas greater activation in either condition across individuals predicted better EF. In addition, there was a general link between activation and planning efficiency (see Table 2), such that increased activation within conditions predicted shorter planning times. Considered together, these findings suggest that the amount of preparatory activation observed in a given condition and individual reflects the outcome of a neural coordination process, and the brain's capacity to configure neural resources involved in complex motor planning. Because planning is more demanding in novel contexts, the neural system is less able to marshal a response in those instances, resulting in reduced peak activation near the time of sequence initiation (see Figure 4). In turn, to the extent that individuals differ in their general capacity to coordinate neural resources during motor planning, better functioning of that same capacity may support better executive functioning.

Integrating the results as a whole, the study suggests that variability in planning familiar sequences primarily reflects lower-level variation in psychomotor speed, the neural substrates of which are not well-captured by peak MRCPs. Conversely, in novel contexts the motor planning system is less readily configured, as indicated by longer planning latencies, reduced activation, and the need for executive resources. Finally, because greater activation in either condition predicts better executive functioning and (gener-

ally) faster planning times, the results suggest that the implicated neural processes are in fact common to both motor planning and broader executive skills, supporting the notion that motor planning represents a rudimentary substrate of higher-order behavioral control (Suchy & Kraybill, 2007).

Returning to the aging and clinical literatures, it may be the case that the effects of greater activation in healthy older adults but reduced activation in various clinical conditions reflect different points along a continuum of neuropathology. That is, the motor planning system may be compromised yet comparatively intact in older adults, thereby enabling compensatory recruitment resulting in greater activation. In contrast, the reduced activation observed in conditions such as Parkinson's disease or patients with focal lesions might reflect impaired capacity due to frank neuropathology and resulting anatomical disconnections. That said, given the fact that most of the MRCP literature (including aging studies) have used motorically simpler tasks such as simple or discriminative RTs (Berchicci et al., 2012; Vallesi & Stuss, 2010), it is unclear whether a capacity model might uniquely apply to more complex motor planning.

Regarding the potential clinical utility of MPLs, the present study clarifies that at least part of the reason for the sensitivity of motor sequencing tasks (and the MPL aspects of those tasks) to executive dysfunction is a result of the inherent novelty of clinically administered measures. In other words, while in the present study the participants were required to overlearn the task, in clinical settings assessment tasks are relatively brief and overlearning is not typically achieved. Nevertheless, refined understanding of the neurocognitive underpinnings of clinical measures is important, and from that standpoint the clinical contributions of the present findings should be acknowledged.

Limitations

Some limitations of this study should also be noted. First, although the study was successful in distinguishing the effect of contextual novelty from possible effects of motor learning implicated in other studies, too few correctly executed novel sequence trials were obtained to permit an investigation of their possibly distinct neurocognitive correlates relative to the contextual manipulation. This limitation was in some sense unavoidable, given that (to our knowledge) this is the first study investigating the Push-Turn-Taptap task using the MRCP approach, and thus a decision was made to prioritize investigating novel context effects based on the prior literature and the need to maintain a reasonable duration of the recording session. Given that the present analogue task elicited robust novel context effects, the current results provide a solid basis for further dismantling research in this area.

Table 6
Hierarchical Linear Regression Predicting Motor Planning Latencies in Novel Contexts

| Step | Variable | R^2 | ΔR^2 | ΔF | df | p |
|------|----------|-------|--------------|------------|------|-----|
| 1 | PS | .15 | .15 | 6.72 | 1,38 | .01 |
| 2 | WM | .15 | .00 | .16 | 1,37 | .69 |
| 3 | EF | .25 | .10 | 4.78 | 1,36 | .04 |

Note. df = degrees of freedom; PS = psychomotor speed composite; WM = working memory composite; EF = executive functioning composite.

Second, given the lack of prior literature on this topic, the current study chose to focus on peak amplitude of the MRCP rather than attempt to differentiate between cognitive correlates of early versus late phases of the potential, as is commonly done in MRCP studies. A review of the grand-average data in Figure 4 appears to further justify this decision, given that only a single negative slope can be observed for the activity in each condition, as opposed to the steeper “negative slope” component that typically distinguishes the early and later phases. That said, given its temporal proximity to the first motor response, the average peak activity measured in this study would nonetheless most likely correspond to the later portion of the classic negative slope component and the motor potential proper (Jahanshahi & Hallett, 2003b). With that in mind, the observed positive relation between peak activation and executive functions seems particularly noteworthy, given that later phases of the MRCP are typically thought to reflect the activity of more primary motor areas, and more movement-specific rather than cognitive effects (Shibasaki & Hallett, 2006), and thus might be expected to relate less strongly to higher-order cognitive abilities.

Third, the p values of the principal findings ranged from .01 to .04. Given that several analyses were conducted, it could be argued that the present results could reflect Type I error due to multiple comparisons. In fact, if strict multiple comparisons corrections were applied, the significance levels would not reach criterion. However, we feel that this issue is considerably tempered by the fact that (a) the results were theoretically consistent, (b) our analyses were highly conservative, examining the contribution of EF only after controlling for other cognitive processes (thereby also necessarily decreasing the degrees of freedom and, consequently, increasing the p values), and (c) the effects were large, with fully between 10% and 18% of unique variance accounted for. Nevertheless, replication with a new sample is warranted.

Fourth, the reliability of the working memory composite was somewhat low in the present sample (.594). Thus, it could be argued that the negative findings for working memory could be a function of low reliability. However, close examination of the results demonstrates that low reliability is unlikely to fully explain our findings. This is because (a) working memory correlated .42 with EF (as would be theoretically expected), but (b) accounted for virtually zero variance in the dependent variables. Importantly, the finding of no contribution from working memory is consistent with theory and a priori expectations.

Last, given the somewhat exploratory nature of the current EEG analogue task, this study did not attempt to characterize the broader neural networks involved in response planning, and thus cannot address potential topographic effects of the two task conditions. Given the many unique features distinguishing the current task from canonical MRCP paradigms (e.g., multiple praxis movements, perceptually complex cues), the current study is perhaps best regarded as providing “proof of principle” for the application of electrophysiology to neuropsychologically representative tasks, and highlights the feasibility of such studies.

Conclusions

In summary, the present study clarifies and affirms the independent contribution of novel context effects to the link between complex motor planning and executive functions. Moreover, re-

sults provided direct physiological support for the contention that motor planning represents a rudimentary substrate of more complex behavioral control, and suggest that peak MRCP activity reflects the capacity of the neural system to configure responses in light of current demands. Future work in this area should explore the neurocognitive correlates of sequence novelty and motor learning in healthy and clinical samples, as well as the detailed network dynamics underlying motor planning effects.

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