Do pursuit movement tasks lead to differential changes in early somatosensory evoked potentials related to motor learning compared with typing tasks?

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Andrew D, Yielder P, Murphy B. Do pursuit movement tasks lead to differential changes in early somatosensory evoked potentials related to motor learning compared with typing tasks? J Neurophysiol 113: 1156–1164, 2015. First published November 26, 2014; doi:10.1152/jn.00713.2014.—Central nervous system (CNS) plasticity is essential for development; however, recent research has demonstrated its role in pathology, particularly following overuse and repetition. Previous studies investigating changes in sensorimotor integration (SMI) have used relatively simple paradigms resulting in minimal changes in neural activity, as determined through the use of somatosensory evoked potentials (SEPs). This study sought to utilize complex tasks and compare separate motor paradigms to determine which one best facilitates long-term learning. Spinal, brainstem, and cortical SEPs were recorded following median nerve stimulation at the wrist pre- and postinterventions. Eighteen participants performed the same paradigms, a control condition of 10 min of mental recitation and two interventions, one consisting of 10 min of tracing and the other 10 min of repetitive typing. Significant increases in the N13, N20, P25, and N30 SEP peaks were seen for both interventions. A significant decrease in the N24 SEP peak was observed for both interventions. Significant improvements in accuracy were seen for both interventions postacquisition but only for tracing during retention. The changes seen following motor learning were congruent with those associated with long-term learning, which was also reflected by significant increases in accuracy during retention. Tracing or the pursuit movement paradigm was shown to be a more effective learning tool. The identification of a task that is sufficiently novel and complex, leading to robust changes in SEP peaks, indicates a task that can be utilized in future work to study clinical populations and the effect of experimental interventions on SMI.

somatosensory evoked potentials; motor learning; sensorimotor integration; cerebellum; retention

THE MALLEABLE NATURE OF THE central nervous system (CNS) enables it to change the way that it responds to subsequent sensory input following periods of altered afferent input (Byl et al. 1997; Classen et al. 1998; Haavik Taylor and Murphy 2007a,b; Murphy et al. 2003; Pascual-Leone et al. 2005; Tinazzi et al. 1998). These use-dependent changes seen following altered afferent input persist even after the input itself has ceased (Byl et al. 1997; Classen et al. 1998; Haavik Taylor and Murphy 2007a,b; Murphy et al. 2003). It is the persistence of these changes that is thought to be necessary for the learning and retention of skill (Nelson et al. 2009), and, as such, input in the form of behavioral training has been utilized to investigate these organizational changes. Many of these studies that investigate these organizational changes have utilized the technique of functional magnetic resonance imaging (fMRI), which measures the activity of neural structures in association with changes in blood oxygenation. This measure provides accurate spatial resolution; however, it is measuring an indirect component of brain electrical activity; in addition to this, it poses difficulty with wait times and is too expensive for routine use in research studies (Pelletier et al. 2007). Plastic changes can also be investigated through electrophysiological techniques such as somatosensory evoked potentials (SEPs), which directly measure the electrical field potentials generated by various neural structures. SEPs provide a measure that offers the highest temporal resolution available in noninvasive investigation, on the order of milliseconds (Walsh and Cowey 2000). Previously, electrophysiological techniques have presented more of a challenge in terms of spatial resolution with relatively large differences between electrodes and sources; the accuracy with which signal sources could be localized was limited, especially with regard to signals generated by deeper structures and complex cortical-subcortical loops (Cebolla et al. 2011). However, localizing techniques such as standardized weighted low resolution brain electromagnetic tomography (swLORETA) have resolved many limitations, such as sensitivity to noise and appropriate inclusion of deep sources allowing for increased confidence and accuracy in the generators of those signals that are measured through electrophysiological techniques (Cebolla et al. 2011). The use of SEPs under varying conditions provides a technique that enables the investigation of immediate changes following sensory processes (Angel et al. 1984). Therefore, this technique can be combined with behavioral input, such as motor learning paradigms, to quantify the activation following training and correlate these with behavioral measures.

Studies have utilized repetitive voluntary movements in combination with SEPs to investigate repetitive muscular activity in humans and its implications on sensorimotor integration (SMI) and have demonstrated alterations in the processing of somatosensory information (Haavik Taylor and Murphy 2007a,b; Murphy et al. 2003; Bossé, 2012; Haavik and Murphy 2013; Andrew et al. 2014). Following the cessation of simple, predictable repetitive typing tasks, changes in cortical SEPs were observed; however, no subcortical changes were seen (Haavik Taylor and Murphy 2007). The use of such a simple task that requires minimal attention results in automatic processing rather than learning. Further clarification of the roles that task characteristics play in learning is needed; therefore, in
a study by Bossé (2012), this same repetitive, predictable task was once again performed with the consideration of behavioral measures such as reaction time and accuracy. In terms of these behavioral measures, while reaction time decreased, accuracy was not seen to change as it was already so high to begin with (Bossé 2012). To change the simple nature of the task, a randomly generated sequence was then used for the typing task and automatically was removed through the use of unpredictable sequences (Andrew et al. 2014). Further changes were now seen in deeper structures and within cerebellar inputs; however, accuracy still did not show an increase. With motor learning, we are observing a process whereby a movement is executed more quickly and accurately with practice; it occurs both spatially and temporally. This sequence only involved three numbers in close proximity to one another and a total of six numbers in each sequence, potentially leading to minimal need for external guidance and thus too simple of a paradigm. Relating back to the point that learning occurs temporally, we see that there is an early fast stage in which improvements in performance occur within a training session and a later slower stage in which further gains occur following a period of consolidation (Doyon et al. 2002; Karni et al. 1998; Nudo et al. 1996). This is associated with retention of the skill, which can be observed in as little as 6–8 h following practice and is associated with motor training paradigms of increased difficulty (Karni et al. 1998; Adams 1987). The assessment of retention is therefore crucial in correlation to neurophysiological changes that may be observed.

When sensory input is used to instruct the generation of motor commands, it involves an overarching process of adaptation, use-dependent plasticity and optimization (Flanders 2011; Krakaeur and Mazzoni 2011). Structures involved in these processes in addition to the primary motor cortex and primary somatosensory cortex include the basal ganglia and cerebellum (Krakaeur and Mazzoni 2011). The utilization of a more complex motor training paradigm in conjunction with electrophysiological and behavioral measures will enable the validation of the roles of not only the cortical but also subcortical and cerebellar regions in relation to the processes of motor learning. Sequence learning tasks have been used extensively to study motor learning; within the realm of sequence learning, the domains of explicit sequences to copy or pursuit movements to follow or trace are commonly utilized. It, however, remains unclear as to whether tracing or copying provides the better training as there has been no interaction between the two tests (Gonzalez et al. 2011).

This study will therefore investigate the interaction between two complex sequence tasks, one tracing and one copying, to determine which is the optimal learning paradigm. In a complex test, an environment is created where automaticity is virtually impossible to develop. By always presenting an unpredictable sequence, the participant is required to use more attentional resources whereby the movement response will no longer be automated. Often, the conclusions of studies posit that tasks utilized were in fact not as complex as first thought due to lack neurophysiological or behavioral changes. This work will utilize two motor tasks that have been previously used in transcranial magnetic stimulation (TMS) studies. If the use of SEPs can support the findings of a parallel technique such as TMS, we can be more stringent in our conclusions in terms of the effects of complexity on motor learning. Baarbé et al. (2014) performed rounds of cerebellar-M1 stimulations before and following motor learning of a typing task that consisted of randomized eight letter sequences of Z, D, F and P. When compared against a control group who did not perform this task, they found reduced cerebellar inhibition following the motor acquisition phase; additionally, significant increases in both reaction time and accuracy were observed, which have not been seen with simpler tasks. The overall purpose for the current study is to determine which learning paradigm would induce measurable neurophysiological changes that also reflected the changes observed in performance. This study provides additional insights into the role that changes in cerebellar pathways may play in motor learning by measuring changes in SEP peaks known to have cerebellar inputs. The previous TMS study (Baarbé et al. 2014) showed a reduction in cerebellar inhibition following motor learning. Given that the cerebellum is heavily involved in coordination, the formation of initial models for motor learning, and the decreased need for the presence of this with learning, the reduced inhibition/input seen with TMS may reflect this. We hoped to see this same effect with SEPs in terms of a decreased amplitude in those peaks known to have cerebellar input, which would now insight into the pathways affected by the changes in cerebellar inhibition.

The goal of training should be pursued with projections to a real world setting. This idea promotes the importance of the level of performance in the long term by examining the effects of separate modalities and their effects on initial learning but also on retention, which has not yet been investigated.

METHODS

Subjects/participants. Eighteen participants with no known neurological conditions, comprised of nine males and nine females (mean age: 22.8; range: 21–25), participated in this study. The study was a paired experimental design where participants were assigned to two different groups of motor training tasks, a typing task and a tracing task, with a minimum of 48 h between sessions. Before the performance of either motor task, control data were collected on each of the participants. Informed consent was obtained and the study was approved by the ethics committee at the University of Ontario Institute of Technology.

Stimulation parameters. The stimuli consisted of electrical pulses that were 1 ms in duration and delivered at rates of both 2.47 and 4.98 Hz through Ag/AgCl ECG conductive adhesive skin electrodes (MEDITRACE 130; Ludlow Technical Products Canada, Mansfield, MA) (impedance <5 kΩ). These electrodes were placed over the median nerve on the skin, 2–3 cm proximal to the distal crease of the wrist, between the tendons of flexor pollicis longus and palmaris longus with the anode proximal on the right arm. This was to allow for movement of the abductor pollicis brevis (APB) through stimulation of the median nerve that primarily innervates this muscle. SEPs were recorded at two different rates to enable optimal conditions to record both the N24 and N30 SEP peak complexes. The use of the slower rate of 2.47 Hz does not lead to SEP peak attenuation, while the faster rate of 4.98 Hz attenuates the N30 SEP peak, allowing for the N24 SEP peak to be accurately identified and measured (Haavik and Murphy 2013; Fuji et al. 1994). Stimuli were delivered at motor threshold for each subject, which is defined as the lowest possible intensity at which a visible muscle contraction of the APB is elicited.

Recording parameters. SEP recording electrodes were placed according to the International Federation of Clinical Neurophysiologists (IFCN) guidelines (Nuwer et al. 1994). Recording electrodes were placed on the ipsilateral Erb’s point, over the CS spinal process.
To ensure that any changes seen were not due to the order of the tasks, the two motor task interventions, either a typing task or a tracing task, were performed in three separate sessions. Before performance of the experimental intervention, control data were collected on each subject. During this time, double baseline measurements were performed for each subject through stimulation of the median nerve at the wrist for pre-SEP measurements, followed by measurements were performed for each subject through stimulation of the median nerve at the wrist for pre-SEP measurements, followed by SEP measurements taken in an identical fashion to the premeasurements. The post-SEPs measurements took 10.13 min at 2.47 Hz and 5.03 min at 4.98 Hz for a total postmeasurement time of 15.16 min. In addition to the SEP measurements, behavioral measurements of accuracy or error rate were also measured pre- and postacquisition phase. After a minimum of 24–48 h following the first session, participants came in for the second session in which they performed the next motor training task. Before performance of the new motor task, a retention test of the task performed 24–48 h before the second session was done. The retention test consisted of simply one posttest of either the typing or tracing task, depending on which one was performed in the first session. During this time, only accuracy was measured. The third and final session occurred 24–48 h following the second session, and this was to administer a retention test of the motor task performed 24–48 h prior. During both tasks, a height adjustable table that had either the keyboard or tracing pad on it was placed at the level of the armrest to eliminate any straining of the wrist or arm to complete the task.

Data analysis. Changes in SEP peak amplitude and latency were measured both pre- and postcontrol and intervention. Additionally, to determine motor training effects, accuracy during the pre- and postacquisition phase as well as postacquisition phase was measured. To ensure that participants were familiarized with the electrical stimulation, sufficient to elicit SEPs, motor thresholding to determine the stimulus intensity that caused movement of the thumb muscle, was performed in addition to a double baseline measurement. Following data collection, SEP peak amplitudes were measured from the averaged 1,500 sweeps of the waveforms.

As two separate tasks were being compared with one another to appropriately compare the differences pre and post the motor training...
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Tasks, data were normalized, being expressed as a proportion of the preintervention baseline so as to make the magnitude of individual measurements of SEP peak magnitude comparable between subjects and groups. This was performed for each of the conditions, precontrol and preintervention (for both typing and tracing) during each session. A mixed measures ANOVA was performed in SPSS, comparing mean SEP amplitude changes with factors of Time (pre and post) and Intervention (control, tracing task, and typing task). Statistical significance was set at 0.05. Only trials that had a stable peripheral nerve volley (N9 SEP peak) were included for statistical analysis. For this criterion to be achieved, the N9 SEP peak was to differ by no more than ±10% pre- and postintervention trials. This ensures that any potential changes observed in the SEP peaks known to have central generators were indeed due to the motor training intervention and not simply due to alterations in afferent input as a result of transient variables such as changes in posture. Following the ANOVA, to discern which groups interactions were specifically between, post hoc comparisons using Tukey’s test were performed.

The amplitudes of the SEP peaks were measured from the peak of interest to the preceding or succeeding peak of opposite deflection in accordance with international recommendations (Nuwer et al. 1994) and previous studies that outline the optimal sites for recording (Cheron and Borenstein 1987, 1991; Rossini et al. 1996; Sonoo et al. 1997; Rossi et al. 2003). The amplitudes and latencies of the following SEP components were identified and measured: the peripheral N9, the spinal N13, the far-field N18 (P14-N18 complex), the parietal N20 (P14-N20 complex) and P25 (N20-P25 complex), the frontal N24 (P22-N24 complex), and the frontal N30 (P22-N30 complex). The latencies were recorded from the time of stimulation onset to their maximal peak or trough for each of the SEP components.

The N24 SEP peak is often observed as a notch that resides on the upward slope of the N30 SEP peak (Garcia Larrea et al. 1992); this particular SEP peak’s amplitude is only measured using the faster rate measurement trials of 4.98 Hz as the higher stimulation rate allows for attenuation of the N30 peak thus allowing for appropriate identification and measurement of the underlying N24 SEP peak (Haavik and Murphy 2013; Fuji et al. 1994).

To investigate and compare the mean difference of accuracy both the pre- and post acquisition phase and during retention of both motor tasks, paired t-tests were performed for both the tracing task and typing task comparing both pre- and postacquisition and postacquisition with retention phase. For the tracing task, accuracy was measured by averaging the distance from each dot the participant’s cursor was for each trial. For the typing task, accuracy was measured based on whether the letter key in the sequence was pressed correctly (1) or incorrectly (0) and this was averaged for each of the trials. Statistical significance was set at 0.05.

RESULTS

All 18 participants who took part in this study were included in the analysis of SEP peaks and in the analysis of behavioral data. No significant changes in latency were seen.

N13 SEP peak (Cv5). The mixed measures ANOVA showed that the mean peak amplitude change for the spinal N13 was significant postmotor learning [F(1,51) = 25.05, P < 0.001], with a significant interaction between factors of Interventions and Time [F(2,51) = 7.98, P = 0.001]. Post hoc analysis showed that for the N13 peak, the interaction exists between the control and tracing groups (P < 0.01). There was a mean decrease of 1% (1.8) following the control vs. a 20.6% (5.6) mean increase following tracing and a 11.6% (3.7) mean increase following typing.

N20 SEP peak (Cc`). The mean peak amplitude change for the parietal N20 was significant postmotor learning [F(1,51) = 43.03, P < 0.001] with significant interactions between factors of Interventions and Time [F(2,51) = 11.22, P < 0.001]. Post hoc analysis showed that this interaction was present between the control and tracing groups (P < 0.001) and between the control and typing groups (P < 0.01). There was a 0.7% (2.2) mean increase following the control vs. a 42.6% (9.9) mean increase following tracing and a mean increase of 32.3% (4.9) following typing.

P25 SEP peak (Cc`). The mean peak amplitude change for the parietal P25 was significant postmotor learning [F(1,51) = 13.5, P = 0.001], with a significant interaction between factors of Interventions and Time [F(2,51) = 3.98, P < 0.05]. Post hoc comparison showed that this interaction exists between the control and tracing groups (P < 0.05). There was a 0.8% (3) mean increase following the control vs. a 26.1% (9.1) mean increase following tracing and a 13.4% (5.3) mean increase following typing.

N24 SEP peak (Fc`). For the frontal N24, the mean peak amplitude change was significant postmotor learning [F(1,51) = 78.46, P < 0.001] with significant interactions between factors of Interventions and Time [F(2,51) = 21.95, P < 0.001]. Post hoc comparisons determined that this interaction was observed specifically between the control and tracing groups (P < 0.001) and between the tracing and typing groups (P < 0.05). There was a mean increase of 1% (1.6) following the control vs. a 29.8% (4.6) mean decrease following tracing and a 16.5% (3.1) mean decrease following typing.

N30 SEP peak (Fc`). For the frontal N30 SEP peak, the mean peak amplitude change was significant postmotor learning [F(1,51) = 91.04, P < 0.001] with significant interactions between factors of Interventions and Time [F(2,51) = 24.08, P < 0.001]. Post hoc analysis showed that this interaction exists between the control and tracing groups (P < 0.001) and between the control and typing groups (P < 0.001). There was a mean increase of 1% (0.9) following the control vs. a 25.5% (4) mean increase following tracing and a 20% (2.3) mean increase following typing. These changes are demonstrated in individual traces for a representative participant in Fig. 2 and in the group mean percent changes seen in Fig. 3.

As previously mentioned, only those trials in which the N9 SEP peak differed by no more than ±10% between pre- and posttrials were included for analysis. In fact, the peripheral N9 SEP peak showed no significant changes following either the control or both of the interventions.

Looking at behavioral data from both the tracing task and the typing task, the paired t-test for the tracing task showed a significant increase in accuracy, P < 0.001 postacquisition phase, and a significant increase in accuracy, P < 0.01 during the retention test (see Fig. 4A). For the typing task, the paired t-test showed a significant increase in accuracy, P < 0.001 postacquisition phase and but no significant change in accuracy during retention (See Fig. 4B).

DISCUSSION

This study has demonstrated that both of the tasks utilized are of increased complexity as seen through both neurophysiological and behavioral characteristics. This work has expanded upon previous work investigating sensorimotor integration following a repetitive typing task that did not exhibit the same complex characteristics (Haavik Taylor and Murphy 2007b; Bossé 2012; Haavik and Murphy 2013; Andrew et al.
This work sought to evolve the characteristics of the motor task used so as to reflect the way that learning occurs, both temporally and spatially. The use of a control group to this study is crucial, seeing that there was a lack of change following no motor training ensures that those changes seen following motor training are in fact a result of a change in CNS processing due to the training task. Previous work, which focused on the effects of simple repetitive movements (Haavik and Murphy 2013; Haavik Taylor and Murphy 2007a,b; Murphy et al. 2003), resulted in minimal changes in sensorimotor processing, although increases in cortical and cerebellar-cortical complexes and changes in intracortical inhibitory processing were observed. However, further research was needed to clarify the role that task characteristics play in determining how well the task is learned, emphasizing the importance of behavioral relevance of the task. Building on this, in a study by Andrew et al. (2014), to change the simple nature of the task, a randomly generated sequence was used; therefore, automaticity was removed through the unpredictable sequences. The motor task sequence showed a significant increase in the N24 peak, which represents neurons within the pathway between the cerebellum and the primary somatosensory cortex (Restuccia et al. 2007). This corroborates findings seen by Haavik and Murphy (2013), suggesting that the cerebellum plays a key role in integrating and learning complex motor tasks, far beyond its role in simple motor tasks. A change in the N30 peak, which represents a complex loop between sensorimotor regions, was also seen, once again suggesting the importance of the unpredictable nature of the task utilized (Andrew et al. 2014). Additionally, behavioral indexes of reaction time and accuracy.
were used. While a decrease in reaction time was seen, accuracy did not change indicating this task was still too simple.

There are numerous motor task paradigms to use when studying the effects of motor learning, of which the most common are the sequential tasks, which include explicit sequences and pursuit movement sequences. Studies have aimed to investigate whether tracing or copying differentially improved learning; it was concluded that the tracing group exhibited superior performance. However, there was no evidence of increased rates of learning as there was no interaction between the two tests (Gonzalez et al. 2011). The current study sought to investigate this through the use of two complex tasks; previous work has often indicated the need to increase the complexity of the tasks whether it is from a lack of change in neurophysiological measures or from lack of improvement in behavioral measures.

Motor performance. In using behavioral input to induce CNS changes in sensory processing, it is crucial that behavioral performance be measured; this was done through observation of accuracy. For both the tracing and typing tasks, there was a significant increase in accuracy following the acquisition phase. However, following a 24- to 48-h period of consolidation, during the retention test, a further significant increase in accuracy was observed only for the tracing task. In previous work that used the technique of SEPs to investigate the effect of a repetitive typing task on SMI, retention was not measured; this study has provided further insight into the learning aspect of the task through measurement of performance 24–48 h later. This provides further evidence for the nature of complexity of both tasks utilized compared with those automatic and predictable tasks that have been observed in previous studies. As can be seen in Fig. 3, the error rates between the two tasks are quite different. While the differences seen in accuracy between the tasks may be in part due to the fact that the complexity of the typing task did not enable discrimination of finer changes, it can be argued that this aspect of the error rate reiterates the complexity of the tracing task as opposed to that of the typing task. With the typing task, there is either a correct key press or an incorrect key press, whereas with the tracing task, there are a multitude of points that one could be off/on the trace, which allows for a greater degree of refinement with performance. This would in turn send larger amounts of feedback when performing the task and allow for greater learning of the skill, as opposed to something much simpler or automatic with typing.

N13 SEP peak (Cv5). The N13 SEP peak is reflective of the activity of the interneurons within the dorsal horn and midcervical cord (Desmedt and Cheront 1981; Sonoo et al. 1991). While there were increases in amplitude for both tracing and typing postacquisition, the change was larger for the tracing group and the interaction was only seen between control and tracing. This finding corroborates other studies that posit that SMI may occur directly at the spinal level whereby sensory input directly affects motor output cells through the α-motor-neurons within the spinal cord (Garcia et al. 1979). Bifurcations may convey the afferent information to a number of locations, and these networks provide a basis for the integration role of the spinal cord. Further evidence for the changes that occur at the spinal level comes from a recent body of research investigating joint dysfunction, more specifically, spinal dysfunction as a state of altered afferent input that can elicit central plastic changes (Haavik and Murphy 2010, 2012). Manipulation of dysfunctional cervical spine joints can alter somatosensory processing (Haavik Taylor and Murphy 2008),
and decreased elbow joint position sense has also been demonstrated in individuals with neck dysfunction (Haavik and Murphy 2011), providing a potential link between N13 changes and performance. The larger increase seen following the tracing task in the current study may be a reflection of increased reliance on proprioceptive input due the increased need for kinesthetic awareness required for task performance.

**N20 SEP peak (C')**. The N20 SEP peak reflects the earliest activity in S1 and is situated in Brodmann’s area 3b (Desmedt and Cheron 1980; Mauguire 1999; Nuwer et al. 1994). Therefore, the similar amplitude increases and interaction for both training tasks demonstrate the role of S1 in motor learning. The parietal P14 peak, measured from the same channel as the N20 peak, is thought to be at a level below the cortex but at or above the foramen magnum (Cruccu et al. 2008; Sonoo et al. 1991). In seeing that this peak remained stable following both tasks, we can be confident in the changes that we see within peaks measured from this same channel and that immediately following the task, we do not see changes at this level. It is possible that SEP measurements might change at a later time point following motor training, but none were seen with the current experimental design.

**P25 SEP peak (C').** The P25 SEP peak reflects neurons that reside within Brodmann’s area 1 of S1 (Mauguiere et al. 1999). The similar increase observed in both tasks following training is once again indicative of the role that the S1 plays in motor learning and sensorimotor integration. Observing that the interaction effect was only seen between the control and tracing and not the control and typing group could be reflective of the fact that the tracing task was more complex in nature.

**N24 SEP peak (F'}).** The N24 SEP peak origination has been localized to near the posterior wall of the central sulcus (Waberski et al. 1999). However, selective N24 SEP peak amplitudes abnormalities in patients with unilateral cerebellar lesions with continued dipole source analysis at the primary somatosensory cortex (S1) have been observed (Restuccia et al. 2007). It is therefore suggested that the N24 reflects the activation of neurons in the pathway between the cerebellum and S1 (Restuccia et al. 2007). The interesting finding with this SEP peak is that there is not only a significant interaction effect between the control and tracing groups but also that there is a significant interaction between the tracing a typing groups. The N24 for both of the tasks decreased, although this decrease was larger for the tracing group. The decrease following learning seen in the peaks for both tasks could be reflective of the role that cerebellar input plays in this cortical peak and in line with previous studies that have proposed a decrease in cerebellar inhibition following motor learning (Baarbé et al. 2014). The cerebellum is involved in coordination; with slow learning patterns, the need for this is decreased and therefore decreases in cerebellar activity have been demonstrated (Miall et al. 2001; Doyon et al. 2003). This is indicative of the learning pattern associated with more complex tasks; the larger decrease seen in the tracing task suggests that this type of task, which provides more of a visuospatial stimulus, is in fact superior to an explicit sequence. Previous work has shown that during initial performance of a coordinated eye-hand tracking task, the cerebellum was significantly activated compared with isolated hand movements (Miall et al. 2001). This activity was decreased following learning more so than following learning of a coordinative tracking task. With visuospatial stimuli, there are larger amounts of initial feedback due to the larger amounts of errors made allowing for continuing gradual improvement. The constrained nature of the typing task does not provide a large gradation of spatial feedback lending to a more automatic performance vs. the learned improvement seen in the tracing task due to that feedback.

**N30 SEP peak (F').** Evidence suggests that the N30 SEP peak is relayed by a complex cortical-subcortical loop that links the basal ganglia, thalamus, premotor areas, and the primary motor cortex (Mauguiere et al. 1983; Rossini et al. 1989, 1987; Waberski et al. 1999). It is therefore suggested that this peak reflects the overarching process of sensorimotor integration (Rossi et al. 2003). The similar increase in amplitude following both motor training tasks suggests that there is an increase in neural activity conducive to those regions involved in SMI. The increase in amplitude seen here compared with the minor increase in amplitude seen by Andrew et al. (2014) with the six-numbered sequences and those studies that observed no change in the N30 with a predictable sequence (Haavik and Murphy 2013) once again validates the role of the N30 SEP complex in SMI and the nature of complexity, specifically in terms of the motor preparation involved for both tasks.

Evidence from previous work indicates that the N30 SEP peak is representative of a complex loop of multiple neural generators (Mauguiere et al. 1983; Rossini et al. 1989, 1987; Waberski et al. 1999). More recent studies have utilized techniques such as whole head EEG with the application of swLORETA as a robust source localization methodology (Cebolla et al. 2014) to further understand the activity and contributions of each structure in this complex cortical-subcortical loop of generators. Cebolla et al. (2011) identified two separate, contextual brain states, one at rest and the other at observation, where they found that for both states the same areas were activated, but characteristic differences in the amount of activity between certain structures were associated with certain brain states. In the current study, the technique of evoked potentials does not allow for determination of which areas within the complex loop of N30 generators change their amount of activation according to differing tasks. Future work using whole head EEG and source localization should be performed to determine this.

In previous work, changes conducive to rapid, or short-term learning were observed both neurophysiologically and behaviorally (Andrew et al. 2014). It was suggested that the development and use of a motor training task with an increased amount of numbers or letters would elicit greater changes reflective of long-term learning, which is what this study has shown.

In comparing two modalities of motor task, this work built on previous studies that investigated whether tracing or copying was a better medium with which to elicit learning (Gonzalez et al. 2011) and was able to have an interaction between the tasks to truly compare the two against one another in the same subjects. It was posited that tracing provides large amounts of continuous feedback that may be beneficiary to learning but that copying explicitly would allow for greater memory in the long term as it forces memorization (Gonzalez et al. 2011). They found that the tracing group exhibited superior performance to the copying group but no real differences in retention following 1 wk. This statement is corrob-
rated by the current study as greater performance was exhibited by the tracing group, and taking both neurophysiological and behavioral measures into account, the tracing task can be seen as the more complex of the two. While copying an explicit sequence, although randomized, relative to the tracing task the spatial and discrete nature of the task, it is much more constrained, ultimately making it easier than and not as novel as the varying frequency and amplitudes presented in the tracing task. This work further demonstrates the potential for the use of SEPs as a tool to investigate the effects of repetitive movement on sensory processing. Further work in which retention tests are performed at multiple time points past 24–48 h along with repeated SEPs measurements would strengthen the implications of a more complex task and its relation to long term learning. One benefit of the tracing task is that it is sufficiently novel so as not to be too easy for experienced typists and musicians, compared with the typing task. Taking this and applying it to a clinical population or following an intervention thought to interfere with motor learning would be beneficial in better understanding the way that these factors may interfere with learning and sensory processing, with the hopes of potential early identification and prevention.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: D.A., P.Y., and B.M. conception and design of research; D.A. performed experiments; D.A. analyzed data; D.A., P.Y., and B.M. interpreted results of experiments; D.A. prepared figures; D.A. drafted manuscript; P.Y. and B.M. edited and revised manuscript; P.Y. and B.M. approved final version of manuscript.

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