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Research report

Creating a movement heuristic for voluntary action: Electrophysiological correlates of movement-outcome learning

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ABSTRACT

Performance of voluntary behavior requires the selection of appropriate movements to attain a desired goal. We propose that the selection of voluntary movements is often contingent on the formation of a movement heuristic or set of internal rules governing movement selection. We used event-related potentials (ERPs) to identify the electrophysiological correlates of the formation of movement heuristics during movement-outcome learning. In two experiments, ERPs from non-learning control tasks were compared to a movement-learning task in which a movement heuristic was formed. We found that novelty P3 amplitude was negatively correlated with improved performance in the movement-learning task. Additionally, enhancement of novelty P3 amplitude was observed during learning even after controlling for memory, attentional and inter-stimulus interval parameters. The feedback correct-related positivity (fCRP) was only elicited by sensory effects following intentional movements. These findings extend previous studies demonstrating the role of the fCRP in performance monitoring and the role of the P3 in learning. In particular, the present study highlights an integrative role of the fCRP and the novelty P3 for the acquisition of movement heuristics. While the fCRP indicates that the goal of intentional movements has been attained, the novelty P3 engages stimulus-driven attentional mechanisms to determine the primary aspects of movement and context required to elicit the sensory effect.

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1. Introduction

Human behavior is effect-oriented; we perform many different types of movements to obtain and respond to a variety of sensory consequences. As a result, the consequences of voluntary behavior are closely monitored and evaluated for future learning (Haggard, 2005). To decide which movements should be selected, it is necessary to acquire a set of efficient rules or a heuristic linking movements and sensory outcomes (cf. Tversky and Kahneman, 1974). We propose that through this close monitoring and evaluation of movement-related outcomes, *movement heuristics* are acquired to guide voluntary behavior.

Previously it has been suggested that voluntary behavior is acquired through a learning process that associates consistently co-occurring movements with their sensory outcomes, the result of monitoring processes initially registering the outcomes of intentional movements (Elsner and Hommel, 2001, 2004; Elsner et al., 2002). The feedback correct-related positivity (fCRP) event-related potential (ERP) is a useful index of the registration of behaviorally relevant sensory outcomes, particularly outcomes related to voluntary movements. In previous studies, the P2a component, occurring in the same time window as the fCRP, has been used to index the occurrence of task or behaviorally relevant stimuli (Potts et al., 2006; Potts, 2004; Potts et al., 1996). The fCRP has been associated with the positive aspect of the feedback error-related negativity (fERN, also referred to as the feedback-related negativity) indicating the achievement of task goals (Hajcak et al., 2006; Holroyd et al., 2008). Additionally, recent studies have demonstrated greater modulation of the related fERN for outcomes linked to voluntary behavior (Bellebaum et al., 2010; Zhou et al., 2010).

For behavior to be voluntary, the consequence of the behavior must be foreseen (James, 1890). However, before a predictive link between intentional movements and sensory outcomes is established through learning (cf. Haggard and Tsakiris, 2009), sensory outcomes are initially unanticipated (Elsner and Hommel, 2001). Along these lines, recent ERP studies have demonstrated that the presentation of an unanticipated sensory outcome following a voluntary response enhances the amplitude of the novelty P3 (Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007). Given that previous studies have demonstrated that the P3 has a unique and predictive role in learning (e.g., Groen et al., 2007; Jongsma et al., 2006; Lindin et al., 2004; Sailer et al., 2010), we proposed that the movement-related novelty P3 is a useful indicator of the learning of a movement heuristic. Indeed, it has previously been suggested that the P3 reflects the updating of an internal model of the movement environment (Krigolson et al., 2008). Therefore, the P3, specifically the novelty P3, is likely to reflect necessary learning processes that evaluate the consequences of voluntary behavior to glean essential associations.

In the present study, we used the fCRP and the novelty P3 to investigate the formation of a movement heuristic to guide voluntary behavior. To differentiate learning a movement heuristic from previous movement-outcome learning paradigms, which establish a simple one-to-one association

between movement and outcome (e.g., Elsner and Hommel, 2001, 2004; Waszak and Herwig, 2007), we developed a novel movement-learning task. In this task, learning did not involve associating the specific mechanics of a movement to a specific outcome, but instead gleaning the principal aspects of the movement(s) eliciting the sensory outcome. Thus the present study aimed to establish electrophysiological correlates of movement-outcome learning. We conducted two experiments in order to elucidate the particular contributions of the fCRP and the novelty P3 for the *learning* of a movement heuristic, and for *monitoring* the outcomes of *voluntary* behavior.

2. Methods

2.1. Participants

A total of 24 students from the University of Otago participated in the present study, with 12 students (five males) in Experiment 1 (aged 20–26, mean age 23 years), and 12 students (five males) in Experiment 2 (aged 19–24, mean age 20 years). All participants were reimbursed NZ\$ 25 to compensate for their time. Prior to the experiment, they were given an information sheet and informed consent was obtained. The Lower South Otago Regional Ethics Committee approved all procedures.

2.2. Stimuli

The stimulus representing the sensory effect was a green circle (2.02°) visual angles) presented in the center of the screen over a central gray fixation cross $(.4^{\circ})$ for 250 msec. The cursor was a gray circle $(.4^{\circ})$ controlled by a tracking-ball mouse. A gray outline of a circle (2.02°) was used in the two non-learning tasks in Experiment 1 to define the specific location (hot spot) on the screen that would elicit the sensory effect when the cursor was moved to the hot spot. The size of the hot spot was the same in the movement-learning task (in both Experiments 1 and 2); however no visual stimulus was presented to define the hot spot (i.e., the hot spot was not visible to the participant).

For the stimulus-response task in Experiment 2, there was no hot spot; timing of the presentation of the sensory effect was computer-controlled and not dependent on the specific movements of the participants. All visual stimuli were presented against a black background on a 54 cm display. MatLab software (MathWorks, Inc., vR2008a) was used for all stimulus presentation and collection of behavioral responses.

2.3. Experimental procedure

2.3.1. Experiment 1

In Experiment 1, the movement-learning task was compared to two non-learning movement tasks with pre-defined movement heuristics. To elucidate the particular contributions of the fCRP and novelty P3 to the learning of a movement heuristic, the movement heuristic employed to elicit the sensory outcome was similar across all tasks. At the start of the experiment, participants were instructed that the goal was

to cause a green circle to appear on the screen by moving the cursor on the screen with a tracking-ball mouse.

For the movement-learning task, participants were not given any specific instructions about how to elicit the green circle. They were instructed that they would learn over the course of the experiment. The green circle was presented when the cursor was moved to within the area of the hot spot (Fig. 1a). After each presentation of the green circle, in all tasks, the cursor was re-positioned to a random starting location on the screen to initiate the same process of learning once again. The purpose of re-positioning the cursor was so that final position (endpoint), and not the initial position of the movement, was the critical determinant of eliciting the presentation of the green circle. The participants were then to repeat the movements required to again elicit a green circle. The hot spot remained constant over the course of a block, but was in a different (randomly-determined) location in each block.

In the first non-learning task (Fig. 1b) a gray outline of a circle was presented prior to start of the task to cue the participants where to move the cursor. Participants were instructed that moving the cursor to the location on the screen defined by the cue would elicit the green circle, but as soon as the block began the cue would be removed. The cue was then removed and participants began this initial-cue task. The purpose of the cue was to provide participants with sensory information to form a movement heuristic prior to the start of the task, thereby serving as a control for the learning of a movement heuristic during the movement-learning task.

To control for any memory processes or uncertainty (particularly with regards to the novelty P3) associated with remembering the cued location in the initial-cue task, a second non-learning task with the gray outline of a circle presented continuously throughout the block was used. At the start of this continuous-cue task, participants were instructed to elicit the green circle by moving the cursor into the location defined by a gray outline of a circle on the screen (Fig. 1c). Thus, sensory information directing participants how to cause the sensory event was provided throughout the continuous-cue task.

For both non-learning tasks (similar to the movement-learning task) the cursor was re-positioned to a different location on the screen following each presentation of the green circle. The location of the hot spot remained constant over the course of a block and varied across blocks. There were three blocks of each task, with 30 presentations of the green circle defining a block. In Experiment 1, a total of nine blocks were conducted, with one block of the continuous-cue task and one block of the initial-cue task following each of the three blocks of the movement-learning task in a counterbalanced design (i.e., ABC-ABC-ABC or ACB-ACB-ACB).

2.3.2. Experiment 2

To specifically investigate the contribution of the fCRP and the novelty P3 for monitoring the outcomes of voluntary behavior to learn a movement heuristic, Experiment 2 compared the movement-learning task to a stimulus-response task in which participants were informed that their movements did not

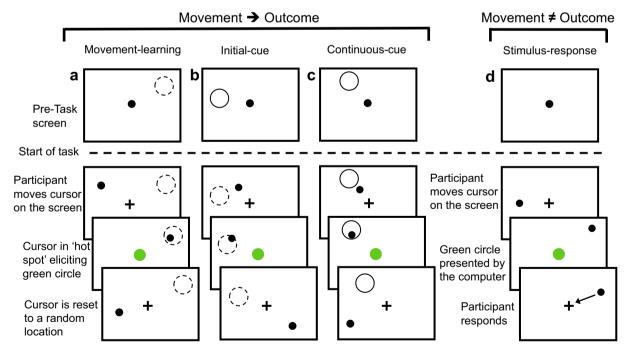


Fig. 1 – Schematic illustration of the tasks used in Experiment 1 (a–c) and Experiment 2 (a & d). The pre-task screen was presented until the participant was ready. For movement tasks (a–c) the participant moved the cursor into the 'hot spot' to elicit the sensory effect. The cursor was then reset and the participant moved the cursor again in the attempt to repeat the elicitation of the sensory effect. In the stimulus-response task (c) the sensory effect was computer-controlled. The participant responded to the green circle by moving the cursor to the fixation cross and then continued to move the cursor in a random fashion. Dashed-line circle indicates the location of the 'hot spot' when it was not visible to the participant and the green circle represents the sensory effect.

elicit the sensory effect. The stimulus-response task also served as a control for the reduction in the inter-stimulus interval observed with learning, which is known to affect P3 amplitude (e.g., Gonsalvez et al., 2007).

The movement-learning task of Experiment 2 was performed in the same manner as in Experiment 1: participants were not given any specific instructions about how to elicit the green circle, and they were told that they would learn over the course of the experiment. A block ended after 30 presentations of the green circle.

Prior to the start of the stimulus-response task, participants were informed that their own movements would not elicit the green circle. Rather, they were instructed to move the cursor around the screen and respond to presentation of the green circle by moving the cursor to the fixation cross and then resume moving the cursor around the screen (Fig. 1d). The timing of the sensory effects in each block of the stimulus-response task was computer-controlled to have the same inter-stimulus interval as the corresponding block of the movement-learning task performed by the same participant (thereby using yoked timing conditions); thus, any variation or decrease in the timing interval of the sensory effects in the movement-learning task would be directly controlled for by the stimulus-response task. A block ended after 30 presentations of the green circle. Five consecutive blocks of the movement-learning task were conducted, rather than interspersed with blocks of the stimulus-response task. This was so that the learning of the movement heuristic through the monitoring and evaluating of the sensory effect would not be interrupted by the stimulus-response task, and to limit confusion about task demands for each condition.

2.4. EEG data acquisition

Electroencephalography (EEG) and electrooculography (EOG) data were collected continuously using a 32-channel Ag–Ag/Cl sintered Quickcap and a Neuroscan Synamps amplifier, interfaced with a Dell Intel computer running Scan 4.3 software. Data were sampled at 1000 Hz with a band pass of .5–200 Hz, and $\times 500$ gain. The 28 scalp electrode sites were referenced to linked mastoid electrodes, with AFz as the ground. Horizontal EOG data were recorded from two electrodes placed on the outer canthi of the two eyes. Vertical EOG data were recorded from linked electrodes on the infraorbital and supraorbital ridges of the left eye. Impedances were maintained below 5 k Ω .

3. Data analysis

3.1. Behavioral analysis

For the movement-learning task (Experiments 1 and 2) and the two non-learning tasks (Experimental 1), the time it took the participants to elicit each green circle was recorded. These times were used to determine hit rate, or the number of green circles presented per 2 sec interval. The hit rate was used as a behavioral measure of the formation of a movement

heuristic and was calculated for the first half of green circle occurrences (1–15; F15) and second half of green circle occurrences (16–30; L15) of each block in order to investigate changes in performance within a block.

3.2. EEG analysis

EEG data analysis was conducted offline using purposewritten MatLab scripts. Continuous EEG data were epoched with respect to stimulus onset (200 msec prior and 1000 msec after the green circle) in the behavioral task, and baseline corrected relative to the 200 msec period prior to stimulus onset. Prior to averaging, epochs containing ocular artifacts were removed using a 'step function' with a 75 μv threshold (Luck, 2005). Data of participants with fewer than 20 trials per block for each task remaining following the artifact rejection process were excluded from further analysis. Two participants in Experiment 1 and three participants in Experiment 2 did not meet this criterion and were removed from EEG analysis. EEG data were then low-passed filtered (30 Hz) using a phase-shift-free Butterworth filter and re-baseline corrected. The mean amplitude of the fCRP was measured at the midline FCz electrode site (located above the presupplementary motor area/supplementary motor area) and averaged across the time window 200-250 msec (Potts, 2004). The mean amplitude of the novelty P3 was measured at the midline Cz electrode site (located above the supplementary motor area/primary motor cortex) and averaged across the time window 300-350 msec (Jentzsch and Sommer, 2001; Polich and Comerchero, 2003). For plotting purposes EEG data were smoothed using a one-dimensional digital filter with a 25 msec time window.

3.3. Statistical analysis

3.3.1. Experiment 1

Hit rates were analyzed using a repeated-measures analysis of variance (ANOVA) with the within-subjects factors task (movement-learning, continuous-cue, initial-cue), block-half (F15, L15) and block (Block 1, Block 2, Block 3). Similar analyses were conducted for the mean amplitude measures of the novelty P3 and the fCRP.

3.3.2. Experiment 2

Hit rates from the movement-learning task were analyzed using a repeated-measures ANOVA with the within-subjects factors block-half (F15, L15) and block (Block 1, Block 2, Block 3, Block 4, Block 5). The mean amplitude measures of the novelty P3 and the fCRP were analyzed using a repeated-measures ANOVA with the factors task (motor learning, motor response), block-half (F15, L15) and block (Block 1, Block 2, Block 3, Block 4, Block 5).

For both experiments, to tease apart specific effects of interactions, additional repeated-measures ANOVAs and planned comparisons were used where appropriate to test our hypotheses. Effects were considered significant if p<.05. Greenhouse—Geisser corrections were applied to p-values, and Bonferroni corrections were applied to pairwise comparisons where appropriate. Effect sizes are shown using partial eta squared (η^2) .

4. Results

4.1. Experiment 1

4.1.1. Behavioral data

The hit rate in each task increased across blocks, and within blocks for the movement-learning task (Fig. 2a and b) and the two non-learning tasks. Verifying these effects, significant main effects of task [F(2,22) = 79.9, p < .001, η^2 = .88], block-half $[F(1,11) = 39.0, p < .001, \eta^2 = .78]$ and block [F(2,22) = 25.8,p < .001, $\eta^2 = .70$] were found, with no significant interactions. Pairwise comparisons for task demonstrated that the hit rate for the movement-learning task [M = .91, SE = .06] was significantly smaller than in the continuous-cue task [M = 1.93, SE = .08, p < .05], and significantly smaller than in the initial-cue task [M = 1.85, SE = .08, p < .05]. ANOVAs for each task with block-half and block as within-subjects factors yielded a significant main effect of block with the hit rate increasing for each task: movement-learning $[F(2,22) = 19.7, p < .001, \eta^2 = .64]$, continuous-cue task $[F(2,22) = 7.6, p < .01, \eta^2 = .41]$, initial-cue task [F(2,22) = 5.6,p < .05, $\eta^2 = .36$]. For the movement-learning task pairwise comparisons for block revealed a significant difference between Block 1 [M = .54, SD = .06] and both Block 2 [M = .94,SD = .11, p < .05] and Block 3 [M = 1.24, SD = .09, p < .001] (Fig. 2a). Only the movement-learning task and the continuous-cue task produced a significant main effect of block-half $[F(1,11) = 59.8, p < .001, \eta^2 = .85 \text{ and } F(1,11) = 13.9,$ p < .005, $\eta^2 = .56$, respectively]. For each block of the movement-learning task there was a main effect of block-half [F(1,11) = 9.0, p < .05, $\eta^2 = .45$; F(1,11) = 24.8, p < .001, $\eta^2 = .69$ and F(1,11) = 18.0, p < .005, $\eta^2 = .62$] indicating task improvement from the first block-half to the last block-half (Fig. 2b).

Post-hoc paired-samples t-tests showed that the change in hit rate within a block was significantly larger for the movement-learning task [M=.50, SD=.46] compared to the continuous-cue task [M=.10, SD=.24], [t(35)=4.4, p<.001] and the initial-cue task [M=-.02, SD=.3], [t(35)=7.6, p<.001] (Fig. 2c). However, post-hoc paired-samples t-tests for the change in hit rate *across* blocks showed no significant difference between the movement-learning task [M=.39, SD=.46], the continuous-cue task [M=.27, SD=.44], and the initial-cue task [M=.27, SD=.39] (Fig. 2d).

4.1.2. fCRP

An fCRP was elicited by all tasks in Experiment 1 (Fig. 3). fCRP amplitude was significantly different across task [F(2,18) = 4.8, p < .05, $\eta^2 = .35$] and block-half [F(1,9) = 7.3, p < .05, $\eta^2 = .45$]. Pairwise comparisons for task demonstrated that the fCRP amplitude in the movement-learning task [M = 8.7 μ V, SE = .7 μ V] was significantly larger than in the continuous-cue task [M = 6.9 μ V, SE = 1.0 μ V, p < .05]. As for the significant main effect of block-half, pairwise comparisons demonstrated that the fCRP amplitude from the first half of a block [M = 8.2 μ V, SE = .9 μ V] was significantly larger than in the second half of a block [M = 6.9 μ V, SE = .8 μ V, p < .05].

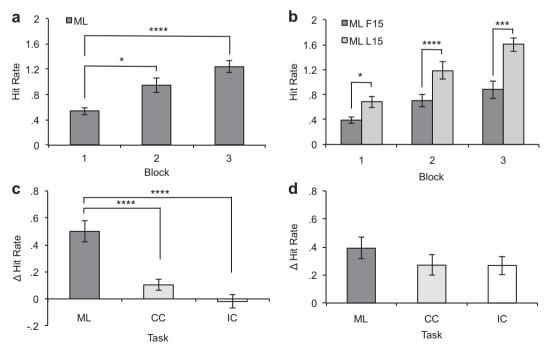


Fig. 2 — Behavioral task performance for Experiment 1. (a) There is a significant improvement in hit rate for the movement-learning task across blocks. (b) Significant increase in hit rate from the first block-half (F15) and to the last block-half (L15) demonstrates improvement within each block. (c) Improvement within a block (change in hit rate) for the movement-learning task (ML) was significantly larger than both the continuous-cue task (CC) and the initial-cue task (IC). (d) Improvement across the blocks was similar for all tasks. *(p < .05), ****(p < .005), and *****(p < .001).

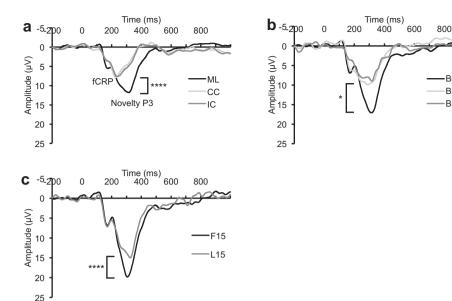


Fig. 3 – Average ERP response to the sensory event at Cz electrode site. (a) Only the movement-learning task (ML) elicited a novelty P3 compared to both the continuous-cue task (CC), and the initial-cue task (IC). No significant difference was found between tasks. (b) Novelty P3 amplitude in the movement-learning task demonstrated learning-related reductions across blocks. (c) Additionally, a significant reduction in novelty P3 amplitude rate from the first block-half (F15) and to the last block-half (L15) indicated improvement within a block. *(p < .05) and *****(p < .001).

4.1.3. Novelty P3

Visual inspection of the ERP waveforms indicated that only the movement-learning task elicited an enhanced novelty P3 component that decreased over the course the experiment (Fig. 3). Verifying this, the corresponding analyses on novelty P3 amplitude yielded significant main effects of task $[F(2,18) = 31.4, p < .001, \eta^2 = .78], block-half [F(1,9) = 22.3,$ p < .005, $\eta^2 = .71$ and block [F(2,18) = 6.7, p < .05, $\eta^2 = .43$] with significant interactions of task \times block-half [F(2,18) = 5.7, p < .05, $\eta^2 = .38$] and task × block [F(4,36) = 4.6, p < .05, $\eta^2 = .34$]. Pairwise comparisons for task indicated that the amplitude of the novelty P3 in the movement-learning task [M = 10.5 μ V, $SE = 1.4 \mu V$] was significantly larger than in the continuouscue task [M = 2.9 μ V, SE = .5 μ V, p < .005] and the initial-cue task [M = 3.5 μ V, SE = .8 μ V, p < .001]. Pairwise comparisons for block-half demonstrated that the amplitude of the novelty P3 in the first half of a block [M = 7.1 μ V, SE = .7 μ V] was significantly larger than in the second half of a block [M = 4.2 μ V, SE = .9 μ V, p < .005]. Pairwise comparisons for block indicated that amplitude of the novelty P3 produced in Block 1 $[M=7.8~\mu V,\,SE=1.1~\mu V]$ was significantly larger than in Block 2 $[M = 4.9 \mu V, SE = .7 \mu V, p < .01].$

ANOVAs for each task with block-half and block as withinsubjects factors yielded a significant main effect of block-half in the movement-learning task $[F(1,9)=31.7,p<.001,\eta^2=.78].$ Pairwise comparisons for block-half demonstrated that the amplitude of the novelty P3 in the first half of a block $[M=13.2~\mu\text{V},\,\text{SE}=1.7~\mu\text{V}]$ was significantly larger than in the second half of a block $[M=7.9~\mu\text{V},\,\text{SE}=1.2~\mu\text{V},\,p<.001]$ (Fig. 3b). A significant main effect of block was found in the movement-learning task $[F(2,18)=7.2,\,p<.05,\,\eta^2=.45].$ Pairwise comparisons for block in the movement-learning task

indicated that amplitude of the novelty P3 produced in Block 1 [M = 15.3 $\mu V,\,SE=2.2\,\mu V]$ was significantly larger than in Block 2 [M = 8.1 $\mu V,\,SE=1.1\,\mu V,\,p<.05]$ (Fig. 3c). A significant main effect of block was also found in the initial-cue control task [F(2,18) = 9.76, $p<.005,\,\eta^2=.52$]. Pairwise comparisons for block in the initial-cue control task indicated that amplitude of the novelty P3 produced in Block 1 [M = 5.2 $\mu V,\,SE=.8\,\mu V$] was significantly larger than in Block 3 [M = 1.7 $\mu V,\,SE=.9\,\mu V,\,p<.01$].

Block 1

Block 2

Block 3

Additionally, a one-tailed Pearson correlation showed that there was a significant negative correlation between novelty P3 amplitude and hit rate for the movement-learning task [r = -.61, n = 60, p < .001].

4.2. Experiment 2

4.2.1. Behavioral data

The hit rate increased within each block and across blocks of the movement-learning task (Fig. 4). The corresponding ANOVA produced significant main effects of block-half [F(1,11) = 50.0, p < .001, $\eta^2 = .82$] and block [F(4,44) = 6.6, p < .001, $\eta^2 = .38$]. Pairwise comparisons for block indicate that there was a significant difference between Block 1 [M = .50, SD = .10] and both Block 4 [M = 1.05, SD = .10, p < .05] and Block 5 [M = .93, SD = .04, p < .01].

4.2.2. fCRP

The fCRP elicited by the movement-learning task was larger than the fCRP elicited by the stimulus-response task (Fig. 5). This was verified by a significant main effect of task on fCRP amplitude [F(2,18) = 4.8, p < .005, η^2 = .35]. Pairwise comparisons for task demonstrated that the fCRP amplitude from the

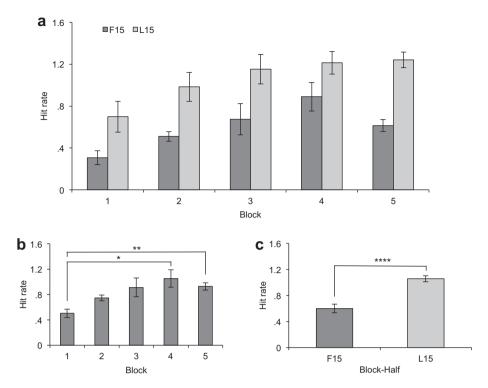


Fig. 4 — Behavioral task performance during the movement-learning task during Experiment 2. (a) A general learning-related improvement in performance task performance can be seen across the five blocks and between the first block-half (F15) and the last block-half (L15) within each block. Improvement in hit rate for the movement-learning task was significant (b) across blocks and (c) within blocks. *(p < .05), **(p < .01), and ****(p < .001).

movement-learning task [M = 8.79 μ V, SE = 1.8 μ V] was significantly larger than in the stimulus-response task [M = 3.92 μ V, SE = 1.6 μ V, p < .005] (Fig. 5).

4.2.3. Novelty P3

In Experiment 2, both the movement-learning task and the stimulus-response task produced novelty P3 waveforms (Fig. 5). Results from the corresponding ANOVA produced significant main effects of task [F(1,8) = 19.8, p < .005, $\eta^2 = .71$], block-half [F(1,8) = 39.4, p < .001, $\eta^2 = .83$], and block [F(4,32) = 5.1, p < .05, $\eta^2 = .39$]. Pairwise comparisons for task demonstrated that the amplitude of the novelty P3 in the movement-learning task [M = 13.0 μ V, SE = 1.8 μ V] was significantly larger than in the stimulus-response task [M = 8.2 μ V, SE = 1.1 μ V, p < .005] (Fig. 5). Pairwise comparisons for block-half revealed that the amplitude of the novelty P3 in the first half of a block [M = 12.6 μ V, SE = 1.3 μ V] was significantly larger than the amplitude of the novelty P3 in the second half of a block [M = 8.6 μ V, SE = 1.1 μ V, p < .001].

ANOVAs for each task with block-half and block as withinsubjects factors yielded main effects of block-half [F(1,8) = 20.1, p < .005, $\eta^2 = .72$ and F(1,8) = 83.9, p < .001, $\eta^2 = .91$] and block [F(4,32) = 3.4, p < .05, $\eta^2 = .30$ and F(4,32) = 3.1, p < .05, $\eta^2 = .28$] for the movement-learning task and the stimulus-response task, respectively. One-tailed Pearson correlations showed a significant negative correlation between novelty P3 amplitude and hit rate for both the movement-learning task [r = -.54, n = 100, p < .001] and the stimulus-response task [r = -.51, n = 100, p < .001].

5. Discussion

In the present study, we aimed to investigate whether ERPs associated with outcome monitoring and evaluation were elicited during the learning of a movement heuristic. To investigate the acquisition of a movement heuristic, we developed a movement-learning task in which participants were instructed to elicit a certain sensory effect but were not informed how. Thus, the movement heuristic for attaining the desired sensory effect was unknown to the participants at the start of the task. The acquisition of a movement heuristic would allow for a shift from broad exploratory movements to efficient movements that consistently result in the presentation of the sensory effect.

The behavioral findings from the present study support this shift, suggesting that the participants formed and refined a movement heuristic for quick and efficient goal achievement. In both experiments, the hit rate in the movement-learning task significantly increased within each block and across blocks. In Experiment 1, the two non-learning tasks also showed significant but moderate improvements in hit rate within and across blocks. However, the movement-learning task demonstrated significantly greater task improvement within each block.

In accordance with the ideomotor theory (e.g., Elsner and Hommel, 2001), the formation of a movement heuristic was controlled by the goals of participants' movements. In the movement-learning task employed in this study, the desired

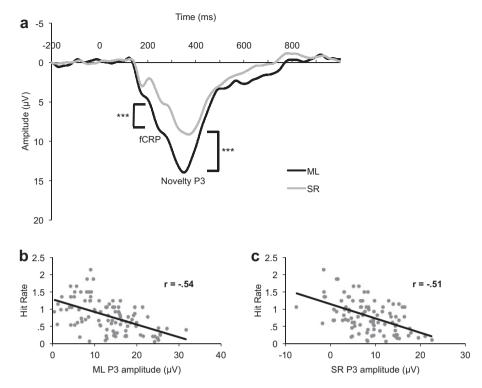


Fig. 5 – Average ERP response to the sensory event at Cz electrode site. (a) Sensory outcomes during the movement-learning task (ML) elicited a larger fCRP and novelty P3 compared to during the stimulus-response task (SR). The novelty P3 from both (b) the ML and (c) the SR demonstrated a significant negative correlation between task improvement measured from the ML, highlighting that reduction in novelty P3 amplitude is associated with a reduction in the inter-stimulus interval.

****(p < .005).

sensory effect was the required end location of the produced movements. Therefore, due to having more than one possible method to reach the end location, learning how to produce the sensory effect was not a simple (or potentially automatic) movement-to-effect association as has been tested in previous studies (e.g., Elsner and Hommel, 2001, 2004). After learning, participants continued to produce movements with the same end location, irrespective of the start position on each trial. Thus, specific motor characteristics did not determine the selection of the movements employed. Rather, it was the utility of the movement to reach a specific location that mattered.

5.1. The fCRP is an indicator of sensory outcomes related to voluntary behavior

The fCRP has been proposed to indicate the achievement of a task goal (Hajcak et al., 2006; Holroyd et al., 2006; Holroyd et al., 2008). In this vein, both the movement-learning task and initial-cue task in Experiment 1 elicited a robust fCRP, and in each of these tasks the sensory effect was the sole indicator that the task goal had been achieved. In the continuous-cue task, however, the continuous-cue also provided feedback regarding achievement of the task goal. Indeed, fCRP amplitude in the continuous-cue task was found to be significantly smaller than fCRP amplitude in the movement-learning task. It has been suggested that the fCRP is modulated by the task or behavioral-relevance of a stimulus (Potts, 2004; Potts et al.,

1996). Along these lines, fCRP amplitude appears to be sensitive to the degree to which the sensory outcome indicates that task goals have been achieved. Additionally, because the fCRP did not demonstrate learning-related changes in Experiment 2, the reduction in fCRP amplitude observed within blocks in Experiment 1 may reflect a general reduction in motivational significance (Sailer et al., 2010). As participants' movements consistently produced the sensory effect the motivation to monitor performance diminished.

Based on the fCRP results from Experiment 2, the abovementioned monitoring processes appear to be more sensitive to the outcomes of voluntary behavior. In Experiment 2, fCRP amplitude was enhanced by sensory effects produced by intentional-based movements compared to the sensory effects that were the imperative stimuli in stimulus-based movements. In both the movement-learning task and the stimulus-response task, participants engaged in voluntary movements prior to the occurrence of the sensory effect. However, in the stimulus-response task, participants were informed that their movements did not cause the presented sensory effect. In other words, the sensory effect was unrelated to the preceding movements. Conversely, in the movement-learning task and the non-learning tasks participants' movements actually elicited the sensory effect. These intentional tasks elicited a robust fCRP. The waveform elicited during the stimulus-response task in Experiment 2, however, was similar in appearance to the waveform elicited by the target stimulus in an oddball-task, in which a P2a precedes the

P3 component (Potts et al., 1996). Thus, the larger fCRP in the movement-learning task compared to the stimulus-response task would indicate that the outcomes of voluntary movement may have more behavioral-relevance because they inform future behavior (Haggard, 2005). Collectively, these findings demonstrate that the fCRP is enhanced by the outcomes of voluntary movement, and may reflect an initial coupling between movements and sensory outcomes.

5.2. The novelty P3 reflects the engagement of evaluative processes for updating movement heuristics

Enhancements in novelty P3 amplitude were observed during the formation of a movement heuristic even after controlling for memory, attentional and inter-stimulus interval parameters. Similar to previous P3 learning studies, we found that with improved task performance there was a significantly correlated reduction in novelty P3 amplitude (e.g., Sailer et al., 2010). By making comparisons between the movement-learning task and the initial-cue task, and between the initial-cue task and the continuous-cue task, we were able to demonstrate that the novelty P3 was more directly related to movement-outcome updating, rather than to memory for the location of the 'hot spot'. Furthermore, by using the stimulus-response task with temporally equivalent occurrences of the sensory effect and heightened attention, we were able to control for the possible influence of a decreased inter-stimulus interval (Fitzgerald and Picton, 1984; Gonsalvez et al., 2007; Gonsalvez and Polich, 2002; Pashler, 1994; Polich, 2007) and stimulus-habituation (Friedman et al., 2001; Kazmerski and Friedman, 1995) to clearly demonstrate the use of P3 as a measure of learning.

Additionally, our results shed light on recent research that has shown an enhancement in novelty P3 amplitude following unanticipated effects elicited by voluntary responses (Iwanaga and Nittono, 2010; Nittono, 2006; Waszak and Herwig, 2007). The novelty P3 elicited in our study, and in those previous studies, reflects the engagement of attentional mechanisms necessary for gleaning primary aspects of movement and contextual information required for understanding the cause of the unanticipated effect. Our own results suggest that over time, the reoccurrence of the novelty P3 provides sufficient information for learning a movement heuristic.

The role of the P3 in facilitating the formation of an accurate movement heuristic is implicated in its function to update current mental schemata (or heuristics) as proposed by the context updating theory (Donchin and Coles, 1988). Similarly, the P3 has previously been proposed to reflect the updating of internal models of the movement environment (Krigolson et al., 2008). Our findings fit with and extend the updating role that the P3 has in guiding future movements. A previous study conducted by Mars et al. (2008) used trial-bytrial analysis of the P3 to demonstrate that the unique information conveyed by a surprising stimulus determines P3 amplitude. A similar process might underlie the present results. With each presentation of the sensory effect, recent movement and contextual information converge in cortical areas. Stimulus-driven attentional processes underlying the novelty P3 are engaged to determine the primary aspects of movement and contextual information. As these primary aspects are gleaned to form a movement heuristic, the unique

information conveyed by the sensory effect reduces, which in turn results in a reduction of the required attentional processes and the resultant novelty P3.

6. Conclusions

These findings extend previous studies demonstrating the role of the fCRP in performance monitoring and the role of the P3 in learning. Additionally, the present study highlights the novel finding of an integrative role of the fCRP and the novelty P3 for the acquisition of a movement heuristic. While the fCRP indicates that the desired sensory effect has been attained, the novelty P3 engages stimulus-driven attentional mechanisms to determine the primary aspects of movement and context required to elicit the sensory effect. By signaling that the preceding movement is coupled with the sensory outcome, processes underlying the fCRP direct novelty P3 attentional processes to evaluate sensory information in light of the preceding movement. Thus, the formation of a movement heuristic is an interaction between performance monitoring, movement-goal coupling, and the evaluation of novel sensory information associated with preceding movements.

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