Unintentional covert motor activations predict behavioral effects: Multilevel modeling of trial-level electrophysiological motor activations

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Abstract

The present experiment measured an EEG indicator of motor cortex activation, the lateralized readiness potential (LRP), while participants performed a speeded category classification task. The LRP data showed that visually masked words triggered covert motor activations. These prime-induced motor activations preceded motor activations by subsequent (to-be-classified) visible target words. Multilevel statistical analyses of trial-level effects, applied here for the first time with electrophysiological data, revealed that accuracy and latency of classifying target words was affected by both (a) covert motor activations caused by visually masked primes and (b) spontaneous fluctuations in covert motor activations. Spontaneous covert motor fluctuations were unobserved with standard subject-level (multi-trial) analyses of grand-averaged LRPs, highlighting the utility of multilevel modeling of trial-level effects.

Descriptors: Priming, Motor activations, Event-related potentials

In the absence of intentional effort or conscious awareness, environmental stimuli to which participants are instructed to ignore may trigger preparatory motor activations (e.g., Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Miller & Hackley, 1992; Osman, Bashore, Coles, Donchin, & Meyer, 1988, 1992). Moreover, even in the absence of an environmental trigger, spontaneous (i.e., more or less random and involuntary) fluctuations in preparatory motor activations may occur (Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). Such preparatory covert motor activations may not be sufficient to trigger overt behavioral responses. Nonetheless, it is widely assumed that they influence the subsequent execution of appropriate responses (e.g., Dehaene, Naccache, Le Clec'H, Koechlin, Mueller, et al., 1998; Eimer & Schlaghecken, 1998, 2003). For example, in speeded two-choice classification tasks, unintentional preparatory motor activations favoring appropriate responses are expected to facilitate the actual execution of such responses. However, those favoring inappropriate responses are expected to interfere with the execution of suitable responses.

Despite extensive theorizing and research, the effects of these preparatory motor activations on task performance have not been clearly established. Past work has relied on standard subject-level analyses that aggregate across trials and across subjects. Such analytic techniques do not afford a clear test of the role of preparatory motor activations on subsequent performance. The present research is the first to use multilevel modeling (MLM) statistical techniques (e.g., Bryk & Raudenbush, 1992; Raudenbush & Bryk, 2002) on single-trial electrophysiological data to establish the impact of unintentional preparatory covert motor activations, both those triggered by environmental stimuli as well as those that occur spontaneously, on subsequent behavior.

Category Priming

Priming tasks are routinely used to assess processes automatically and unintentionally triggered by environmental stimuli (e.g., Ferguson & Zayas, 2009). In the standard category priming paradigm, participants classify visible target words that are dichotomized on a dimension (e.g., gender) into one of two categories (i.e., male vs. female). Prior to the presentation of targets, masked prime words from one of the two categories are presented. A robust finding from studies using this kind of procedure is the *priming effect* (e.g., Dehaene et al., 1998; Fazio, 2001; Greenwald, Draine, & Abrams, 1996). When primes and targets are congruent (both belong to the same category), classification of targets is facilitated, as reflected by higher accuracy, faster reaction times, or both. When primes and targets are incongruent (belong to opposing categories), classification of targets is more difficult.

PSYCHOPHYSIOLOGY

Historically, priming effects, especially those obtained from lexical decision tasks that call for word versus nonword judgments, have been interpreted as reflecting spreading semantic activation (Fazio, 2001). Upon the presentation of a prime, corresponding nodes within a person's lexical–semantic network automatically become activated. In turn, this activation spreads throughout the network to associated nodes, including those corresponding to concepts that are related to the prime. Thus, a target that belongs to the same category as the preceding prime will be identified with greater ease, because nodes associated with the target have already been activated to some extent. A target that belongs to the opposing category as the preceding prime will not benefit from the spreading semantic activation caused by the prime.

Although spreading semantic activation is still the most widely accepted account for priming, a growing body of research (e.g., Dehaene et al., 1998; Klinger, Burton, & Pitts, 2000; Praamstra & Seiss, 2005) supports the idea that category priming effects are caused, at least in part, by a process of response competition (see also Fazio, 2001). When the target classification task has a limited set of response options (male vs. female) and when primes are classifiable using those same responses, subjects will unintentionally apply the task instructions to the primes. As a result, the primes themselves will trigger preparatory motor activations that either facilitate or interfere with the classification of subsequently presented targets.

Lateralize Readiness Potential (LRP) as a Measure of Covert Motor Activations

Increasingly, researchers have been using electrophysiological measures to investigate motor activations triggered by environmental stimuli. The lateralized readiness potential (LRP) is an electroencephalographic (EEG), millisecond-to-millisecond, continuous record of the differential activation of the motor circuits responsible for controlling hand movements (e.g., Van Turennout, Hagoort, & Brown, 1998). Critically, the LRP captures "subthreshold" response activations, that is, low levels of preparatory covert motor activations that precede overt behavioral responses (Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988).

Research using LRP consistently shows that stimuli that participants are instructed to ignore trigger covert motor activations (Coles et al., 1985; Miller & Hackley, 1992; Osman et al., 1988, 1992). Most relevant, using a masked priming task, Dehaene and colleagues (1998) showed that the direction of the initial covert motor activation was driven by the information provided by the prime. That is, congruent primes, which cued the same response as targets, triggered preparatory covert motor activations towards correct target responses. In contrast, incongruent primes, which cued the opposite response as targets, triggered preparatory motor activations towards incorrect target responses. These prime-induced preparatory covert motor activations occurred prior to the motor activations triggered by the presentation of the target. Moreover, analyses of reaction times revealed the expected behavioral priming effect (i.e., slower RTs on incongruent trials than congruent trials). Jointly, these LRP and behavioral data suggest that prime-induced preparatory covert motor activations interfered with or facilitated the execution of appropriate responses to subsequent stimuli (e.g., Eimer & Schlaghecken, 1998, 2003; Minelli, Marzi, & Girelli, 2007; Praamstra & Seiss, 2005).

Even more, Gratton and colleagues (1988) have shown that prestimulus preparatory covert motor activations also influence subsequent behavioral responses. Specifically, in a two-choice con-flict task (i.e., flanker; Eriksen & Eriksen, 1979), participants classify the central letter of a five-letter array (e.g., HH*H*HH, HH*S*HH). On "fast guess" trials in which participants responded within 150–199 ms of the presentation of the array, covert motor activations during the 100-ms fore period (the time preceding the onset of the stimulus array) predicted the subsequent behavioral response.

Collectively, these findings suggest that changes in preparatory covert motor activations, as indexed by the LRP, may be unintentionally triggered by a prime stimulus, or reflect spontaneous (more or less random) fluctuations in motor readiness. Most importantly, they appear to play a role in the execution of subsequent behavioral responses.

Trial-Level Effects of Covert Motor Activations on Subsequent Performance

Although the existing work is consistent with the hypothesis that preparatory covert motor activations, whether prime-induced or spontaneous (more or less random), precede and impact behavioral performance on individual trials, the analytic techniques that have been used do not afford a clear test of this hypothesis. Research to date has used standard statistical procedures of aggregating data across participants and across trials for a given participant. However, such subject-level analyses do not unequivocally establish that preparatory covert motor activations and subsequent behavioral performance occur in known sequence on individual trials. It is possible, for example, that they are parallel effects with covert motor activations occurring for a subset of participants and behavioral priming effects occurring for a different subset, or that within the same participant, covert motor activations occur on a subset of trials and behavioral priming effects occur on a different subset.[1]

According to various models of continuous (vs. discrete) human information processing models (McClelland, 1979; Miller, 1988; Sternberg, 1969), environmental stimuli trigger a number of psychological processes (e.g., motor, semantic) likely operating, at least at times, in parallel. Thus, it is possible that the extent to which primes impact subsequent performance via motor activation, semantic activation, or a combination of both may vary from trial to trial within an individual or across individuals. This, in turn, may lead to behavioral effects occurring on some trials and covert motor activations occurring on different trials. For example, prime-induced covert motor activations may quickly dissipate given the short-lived nature of prime influence (Greenwald et al., 1996) and return to baseline levels before influencing performance on the subsequent target classification task. In this case, behavioral effects may still emerge, if primes exert their influence through other mechanisms (e.g., semantic activation).

Present Research

A test of the hypothesis that covert motor activations influence subsequent behavioral performance requires a shift from traditional subject-level, multitrial-aggregation analyses to trial-level analyses. In the present research, we used MLMs, a statistical technique well suited for investigating trial-level effects of motor processes on subsequent response. Although MLM techniques have been used extensively in a number of psychological domains

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[1]Analyses that involve sorting trials into bins (e.g., as a function of response time) also rely on standard subject-aggregate analyses, because data are averaged across subjects. Moreover, a characteristic of binning trials is that multiple trials from a given subject may be included in a bin, thereby violating assumptions of independence that are central to standard subject-aggregate statistical techniques.

(e.g., Zayas & Shoda, 2007; see also Bolger, Zuckerman, & Kessler, 2000), they have not been applied to electrophysiological data. The present paper is the first application of MLM to electrophysiological data for the purpose of modeling the effect of covert motor activations, on a given trial, on later performance outcomes; how these covert motor activations interact with, depend on, prime information; and the strength of these associations as they unfold over time.

Method

Overview of Procedures

Participants completed all procedures individually on an IBM compatible desktop running Inquisit psychological software (Millisecond Software, LLC, Seattle WA). CRT monitors operated at a 120-Hz refresh rate. Participants completed a category priming task followed by a perceptibility task while their EEG was recorded.
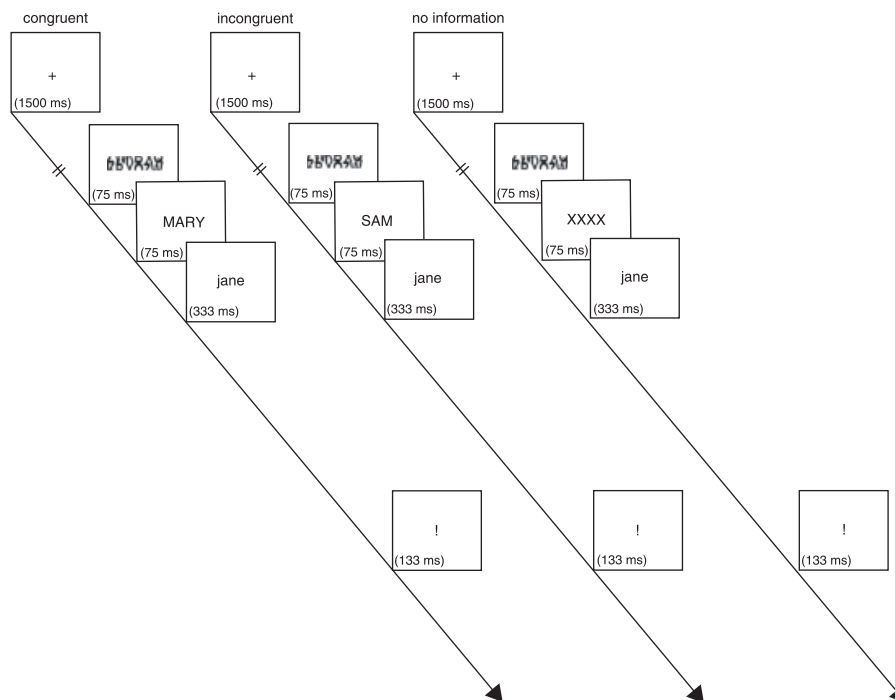
Participants

Sixteen participants (9 female) completed the experiment in exchange for extra credit applied towards their introductory psychology courses. Participants had normal or corrected-to-normal vision.

Category Priming Task

Participants' task was to classify the gender of visible male or female proper names (targets) presented in the center of the computer screen by pressing the E key with a finger from their right hand and the I key with a finger from their left hand. As shown in Figure 1, each target was preceded by a prime stimulus for 75 ms, which itself was preceded by a forward mask presented for 75 ms. There were no additional time intervals between stimuli. Participants indicated their response to the target within a 133-ms interval called the response window. The response window obliges participants to classify targets within a specified window of time, thus making individuals respond more quickly than they normally would be inclined to do. Thus, the response window increases participants' reliance on prime information and increases the likelihood that a response will occur before the rapid decay of activation from the masked prime (e.g., Greenwald, Abrams, Naccache, & Dehaene, 2003). In block 1, the onset of the response window was 333 ms post target onset, and was delayed by 33 ms in each subsequent block.[2] During the response window, a gray exclamation point ("!") appeared on the computer screen. If participants indicated their response within the response window, the exclamation point turned red. On average, participants indicated their response within the response window on 62% of the trials ($SD = 4\%$) and indicated their response prior to the offset of the response window on 87% of the trials ($SD = 13\%$). The intertrial interval (ITI) was 1500 ms, during which a focus point (+) appeared on the computer screen. These specifications (Stimulus Onset Asynchrony (SOA) of 75 ms, prime duration of 75 ms, and response window procedure) have been shown to maximize the effect of the prime on the target classification task (Greenwald et al., 1996; Klinger et al., 2000).

The category priming task consisted of three types of trials: congruent (prime and target belonged to the same gender category), incongruent (prime and target belonged to opposite gender categories), or no-information (prime was a letter string

Figure 1. Schematic representation of temporal structure of category priming task for congruent, incongruent, and no-information trials. Duration of each stimulus (in milliseconds) is in parentheses. Participants indicated their response to the target within a 133-ms interval called the response window. During the response window, a gray exclamation point appeared on the computer screen. If participants indicated their response within the response window, the exclamation point turned red. In block 1, the onset of the response window was 333 ms post target onset, and was delayed by 33 ms in each subsequent block.

"XXXX"). Participants completed two 24-trial and two 48-trial practice blocks followed by six 48-trial data blocks. Targets were presented in lowercase Arial font, and primes were presented in uppercase Arial font. Two sets of 12 male and 12 female proper names were used as stimuli. Stimulus set and response key assignment were counterbalanced across participants. To minimize blinking and other motor movements that would produce artifacts in the EEG recording, participants were instructed to minimize blinking throughout the experimental procedures and to blink in between blocks and in between trials (during the ITI).

Perceptibility Task

To assess the extent to which the masked primes were perceptible, participants completed a perceptibility task. This task was identical to the category priming task except that the participants' task was to classify the gender of the prime and make their response after the end of the response window. The perceptibility task consisted of two 48-trial practice blocks and six 48-trial data blocks. Analyses of accuracy (excluding trials with reaction times (RTs) > 5000 ms) showed that primes were partially perceptible, but clearly difficult to identify (accuracy = 63%, $d' = .76$, $t(15) = 5.07$, $p = .0001$).

EEG Recording
EEG was recorded using tin electrodes attached to an elastic cap (Electro-Cap International, Eaton, OH) placed over the left and right pre-frontal (Fp1, Fp2), frontal (F3, F4), inferior frontal (F7, F8), temporal (T7, T8), central (C3, C4), parietal (P3, P4), posterior parietal (P7, P8), and occipital (O1, O2) locations, and from three midline locations (Fz, Cz, Pz). Given the aims of the present research, we focused specifically on C3 and C4. Vertical and horizontal eye movements were recorded via electrodes placed below the left eye and to the right of the right eye, respectively. The double subtraction method used to derive the grand-averaged LRPs and the single subtraction method used to derive the trial-level covert motor activations (both described in the *Data Reduction and Analytic Strategy* section) alleviate activity caused by eye, muscle, and other motor-related artifacts. All channels were referenced to an electrode placed over the left mastoid bone. Activity recorded over the right mastoid was not affected by trial type. The EEG was amplified (SAI bioamplifier system) with a bandpass of .01–100Hz (3dB cutoff). The EEG and stimulus trigger codes were digitized on-line by a Data Translation 2801-A board at a sampling frequency of 200 Hz.

Data Reduction and Analytic Strategy

Behavioral data. Reaction times and accuracy were recorded for each trial. Trials with response latencies outside the normal range of time needed to categorize a single trial (i.e., greater than 1000 ms for the category priming tasks and greater than 5000 ms

for the perceptibility task) were excluded from all analysis. Analyses of reaction times were based on log-transformed reaction times for correctly classified targets only. Reaction times transformed back to milliseconds are reported for illustrative purposes.

To investigate category priming effects on accuracy, we analyzed proportion incorrect as a function of trial type. Additionally, we used a signal detection approach, which takes into account responding biases, to corroborate results from analyses based on proportion incorrect. We computed signal detection theory's sensitivity (d') measure by treating trials for which the prime belonged to the category female as signal trials and those for which the prime belonged to the category male as noise trials. The hit rate was thus the proportion of signal trials classified as female, and the false alarm rate was the proportion of noise trials classified as female. Similar analyses were conducted to assess performance on the perceptibility task.

Grand-averaged LRPs. Given the focus on prime-induced activations, grand-averaged LRPs were time-locked to primes, and the 100-ms period preceding prime onset was used as a baseline. We computed the LRP following procedures described by Van Turennout and colleagues (1998):

$$LRP = mean(C3 - C4)_{RH} - mean(C3 - C4)_{LH} \qquad (1.0)$$

where RH represents trials in which the correct target response cued the right hand, and LH represents trials in which the correct target response cued the left hand. On each trial, for each sample point, the difference between potentials recorded from electrode sites placed over the left and right central medial-lateral sites (C3, C4) were averaged separately for trials in which the target stimulus called for left- and right-hand responses. The difference waveform obtained for left-cued trials was subtracted from the difference waveform obtained for right-cued trials.[3] Thus, negative-going LRPs indicate covert activations of the correct response, and positive-going LRPs indicate covert activations of the incorrect response.

Two-tailed t-tests were performed on voltage sampled every 5 ms. The LRP was defined as being present if the t-tests performed on five or more consecutive 5-ms samples were statistically different from zero in the same direction. The onset of the LRP was taken as the beginning of such a sequence (Van Turennout et al., 1998).

Trial-level covert motor activations. Trial-level covert motor activations (referred to hereafter as TCMA) were assessed by computing, for each trial, the difference between potentials at C3 minus potentials at C4 (Gratton et al., 1988).[4] Trials in which the target cued the left-hand were multiplied by -1. Sixty-ms moving averages of this difference were computed, each shifted by 5

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[2]The 33-ms incremental delay in the response window was included to investigate whether allowing participants more time to respond would weaken the influence of the prime. Analyses of the grand-averaged LRPs as well as the trial-level covert motor activations revealed no appreciable effect of delaying the response window. At the behavioral level, the magnitude of the priming effect decreased linearly as the response window was delayed (error rates: ($F(1,15) = 4.91$, $p = .043$, $\eta^2 = .25$; reaction times: ($F(1,15) = 34.51$, $p = <10^{-4}$, $\eta^2 = .70$), although priming effects were statistically significant in each data collection block. Because the delay of the response window did not reliably influence covert motor activations, which are the focus of the present research, we report results of analyses collapsing across block.

[3]There are a number of methods available for computing the LRP. The method used in the present research is equivalent to procedures used by De Jong, Wierda, Mulder, and Mulder (1988) and Eimer and Schlaghecken (1998), except that it reverses the polarity. It is also equivalent to other methods (e.g., Coles, 1989; Gratton et al., 1988) that divide the entire sum by 2, thus halving the amplitude.

[4]Conventional subject-level LRP involves the subtraction of average voltages recorded at C3 and C4 with left and right hand responses (or equivalent procedures). This subtraction removes lateralizations caused by structural and functional differences between the two hemispheres that are not related to motor lateralizations. To compute TCMA, we followed Gratton et al. (1988)'s method of assessing laterality on a given trial. Specifically, we subtracted voltages recorded at C3 and C4 on a given trial.

ms (0–59 ms, 5–64 ms, etc.). Temporal positions of TCMA are identified by the midpoints of these 60-ms intervals. Each trial consisted of 220 TCMA 60-ms intervals, with the first of these intervals starting at -100 ms (-130 ms to -71 ms) post prime onset and the last ending at 1000 ms (970 ms to 1029 ms) post prime onset.

MLM of trial-level effects of covert motor activations. The data from the present study are multilevel in that all trials, the level-1 units, were presented to each participant, the level-2 units. MLM (e.g., Bryk & Raudenbush, 1992; Raudenbush & Bryk, 2002) can estimate the relations among constructs at level 1 and level 2 simultaneously, while taking into account that the observations at level 1 are not independent. Accordingly, MLM is appropriate for estimating the effect of TCMA on subsequent response (accuracy and response time). Below, we describe the MLM analyses with accuracy as the outcome. We repeated the MLM analyses treating raw reaction time as the outcome variable (results using log-transformed reaction time were highly similar to those observed with raw reaction time).

We first performed MLM to estimate the effect of each 60-ms TCMA interval on accuracy on a given trial for each of the three trial types separately. The level-1 model estimated, for each participant j ($j = 1$–16), a regression line that predicted each participant's accuracy (correct = 0; error = 1) on each trial i from the subject-centered 60-ms TCMA interval. This model was represented as follows:

$$[error_i]_j = b_{0j} + b_{1j}[TCMA_i] + r_{ij} \tag{2.0}$$

where b_{0j}, the intercept, is interpreted as participant j's mean error rate for a given trial type (because all level-1 predictors were subject-centered); b_{1j}, the slope, represents the effect of the 60-ms TCMA interval on accuracy for each participant j (positive coefficients represent the predictive magnitude of TCMA on correct target response for a given participant); and r_{ij} is the residual error term.[5]

The level-2 models estimated the average effects for the entire sample. The models were represented as follows:

$$b_{0j} = \gamma_{00} + \mu_{0j} \tag{2.1}$$

$$b_{1j} = \gamma_{10} + \mu_{1j} \tag{2.2}$$

where the intercept, γ_{00}, is interpreted as the average error rate for the entire sample; γ_{10} is the average effect of TCMA on error (positive coefficients represent the predictive magnitude of TCMA on correct target response for the sample as a whole), and thus the primary estimate of interest; and μ_{0j} and μ_{1j} are the residual error terms. Note that, because we did not hypothesize differences among participants, no predictor variables were included in the level-2 models.

Second, we performed MLM to investigate how the effect of TCMA on subsequent behavioral response varied across trial types. A set of priori contrasts was created to test the effect of each trial type relative to the other two. For these analyses, the level-1 model was identical to the previous model (2.0), except that it also included a contrast code for trial type and the trial type contrast × TCMA interaction term as level-1 predictors.

Accordingly, the level-2 models from these analyses estimated the average effects for the entire sample, and provide a test of whether the effect of TCMA varies across trial types.

Results

Behavioral Priming Effects
Analyses of the behavioral data showed the expected priming effects; task performance was facilitated on congruent trials and hindered on incongruent trials (Table 1). Compared to no-information trials, incongruent trials produced more errors, $t(15) = 10.77$, $p = 10^{-7}$, and slower responses, $t(15) = 9.57$, $p = 10^{-7}$. In contrast, compared to no-information trials, congruent trials produced fewer errors, $t(15) = 2.16$, $p = .048$, and faster responses, $t(15) = 3.93$, $p = .001$.

To assess the magnitude of masked priming effects when prime perceptibility was zero, we followed Draine and Greenwald's (1998) procedure of regressing priming effects on perceptibility effects, both measured in d'. The unstandardized intercept, an index of priming in the absence of prime perceptibility, was .56 and statistically greater than zero, $t(15) = 8.27$, $p < .0001$.

Evidence of Prime-Induced Covert Motor Activations: Grand-Averaged LRPs
Before investigating TCMA effects, the grand-averaged LRPs, which reflect motor activations averaged across trials and across participants, were examined. Figure 2a shows the grand-averaged LRPs for all (i.e., correct and incorrect) trials as a function of priming conditions. Negative-going (upward) LRPs indicate activation of the correct response. Positive-going (downward) LRPs indicate activation of the incorrect response (see *Method* section for a description of the statistical analyses).

On congruent trials, primes tended to trigger covert motor activations associated with the correct target response, whereas on incongruent trials, primes triggered covert motor activations associated with the incorrect target response. Evidence for this inference is based on the onset and initial direction of the LRPs for the three trial types. Specifically, the LRP for congruent trials was negative-going, indicative of covert activations of the correct target response, starting at 335 ms post prime onset. In contrast, the LRP for incongruent trials was positive-going, indicative of covert activations of the incorrect target response, starting at 340 ms post prime onset. Moreover, the LRP onsets for congruent

Table 1. *Mean Error Rate (i.e., Proportion Incorrect) and Reaction Times (in Milliseconds) as a Function of Trial Type (Congruent, No-Information, and Incongruent)*

Trial Type	Error Rate (proportion incorrect)		Reaction Times (ms)	
	M	(*SD*)	*M*	(*SD*)
Congruent	.12$_a$	(.07)	472.72$_a$	(29.65)
No-information	.15$_b$	(.08)	486.71$_b$	(26.35)
Incongruent	.29$_c$	(.10)	518.02$_c$	(32.24)

Note: Means with different subscripts differ significantly (*p*s for differences between means ranged from 10^{-7} to .05). Analyses of reaction times were based on log-transformed reaction times for correctly classified targets only. Reaction times transformed back to milliseconds are reported for illustrative purposes. SD: standard deviation.

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[5]A fixed slope effect for TCMA was specified for all models after ascertaining, using the log likelihood ratio test (Bryk & Raudenbush, 1992), that allowing individual-subject slopes to vary did not significantly increase model fit.

and incongruent trials occurred approximately 65–70 ms earlier than the LRP onset for no-information trials, which was negative-going at 405 ms post prime onset. The 65–70 ms delay in LRP onset for no-information trials relative to the onset for congruent and incongruent trials corresponds with the 75 ms prime–target SOA.
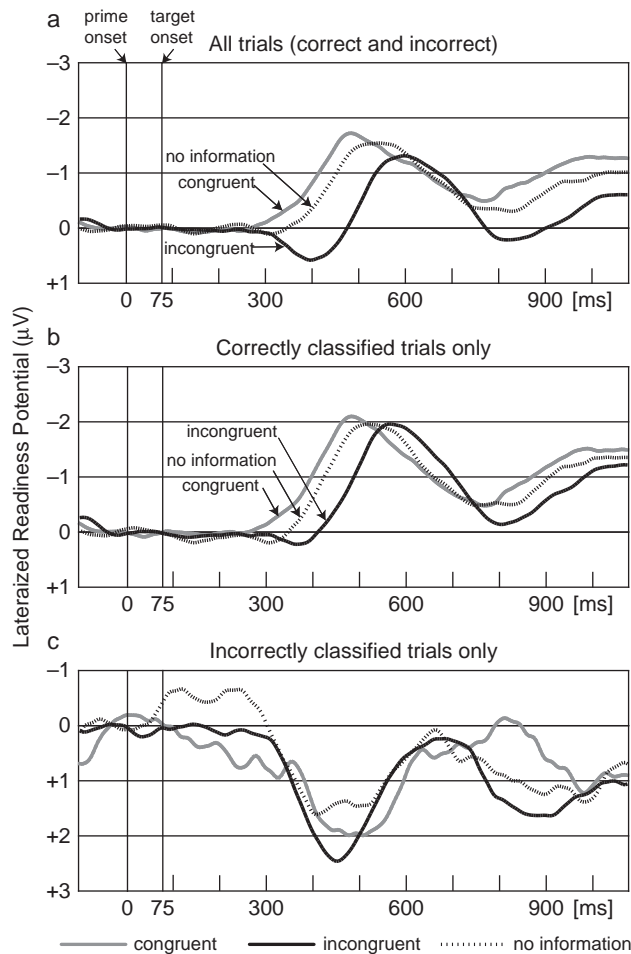
Figure 2. Grand-averaged lateralized readiness potential (LRP) waveforms. LRP waveforms are shown for (a) all trials (correctly and incorrectly classified), (b) correctly classified only, and (c) incorrectly classified only. In each panel, LRPs are plotted as a function of trial type: Congruent, incongruent, and no-information. Arrowheads mark the onset of the LRP for each trial type (i.e., the first of five or more consecutive 5 ms samples in which the LRP was statistically different from zero in the same direction). LRPs are time-locked to prime onset, which is marked by a vertical line at 0 ms. The vertical line at 75 ms post prime onset marks the onset of the target. LRPs deviate from the baseline (zero) as response preparation occurs. LRPs in the negative (upward) direction reflect activation of the contralateral motor cortex, indicative of preparing to make a correct target response. LRPs in the positive (downward) direction reflect activation of the ipsilateral motor cortex, indicative of preparing to make an incorrect target response. LRP waveforms were derived by (1) computing the difference between potentials recorded from electrode sites placed over the left and right central medial-lateral sites (C3–C4), (2) creating separate averages for trials in which the target stimulus called for left- and right-hand responses, and (3) subtracting the difference waveform obtained for left-cued trials from the difference waveform obtained for right-cued trials.

Prime-induced covert motor activations were substantial, as indicated by comparing the grand-average LRP for congruent and incongruent trials to that for no-information trials. At 405 ms post prime onset, the time at which activation of the correct response begins to be detectable on no-information trials, the incorrect response was still activated on incongruent trials as reflected by a statistically significant positive-going LRP. Moreover, at 405 ms post prime onset, the correct response was activated to a greater extent on congruent than no-information trials, $t(15) = 3.74$, $p = .002$.

The pattern of the grand-averaged LRP data on correctly classified trials (Figure 2b) was similar to those based on all trials, with one exception: analysis of the LRP revealed that correctly classified incongruent trials did not show significant activations of incorrect responses. The LRP for correctly classified incongruent trials was never significantly greater than zero. Nonetheless, the temporal order of LRP onsets as a function of trial type was similar to the pattern observed for analyses involving all (correctly and incorrectly classified) trials. Covert motor activations of the correct response occurred at 330 ms post prime onset on congruent trials, at 370 ms on no-information trials, and 430 ms on incongruent trials.

On incorrectly classified trials, the pattern of the grand-averaged LRPs was approximately the mirror image of that for correctly classified trials (Figure 2c). Because LRPs for incorrectly classified trials were based on considerably fewer trials (see Table 1), they were less statistically detectable. Thus, the fluctuations in the LRP waveform < 300 ms post prime onset were not statistically different from zero. Nonetheless, the sequence of covert motor activations suggests prime influence. On incongruent trials, in which primes cued the incorrect target response, the LRP onset of the incorrect response was positive-going and statistically reliable at 340 ms, whereas, on no-information and congruent trials, the LRP onset of the incorrect response was delayed by 40 ms and 50 ms, respectively.

Multilevel Analyses of Covert Motor Activations on Performance
Analyses of grand-averaged LRPs are based on covert motor activations aggregated across trials and across participants. The standard practice of multitrial aggregation allows for the possibility that prime-induced covert motor activations occur on a subset of trials (or a subset of participants), and behavioral priming effects occur on a different subset (or other participants). In contrast to standard subject-level aggregation analyses, MLM estimates, for each trial, the effect of covert motor activations on subsequent response. In the present research, MLM was used to examine the effect of covert motor activations on subsequent response, how covert motor activations interact with prime information to influence behavioral responding, and the strength of these associations as they unfold over time (see *Method* section for a description of the analyses).

Predicting accuracy from trial-level covert motor activations. The level-2 model provides an estimate (γ_{10} in equation 2.2) of the average effect of TCMA on error. Figure 3a plots the t values corresponding to γ_{10}, and reflects the predictive ability of each 60-ms TCMA interval over time for each trial type separately. A positive t value indicates that greater covert motor activations of the correct (vs. incorrect) response predicted greater accuracy. A negative t value indicates that greater covert motor activations of the correct response predicted decreased accuracy.

A noticeable effect in Figure 3a is the difference in the predictive ability of covert motor activations on accuracy between
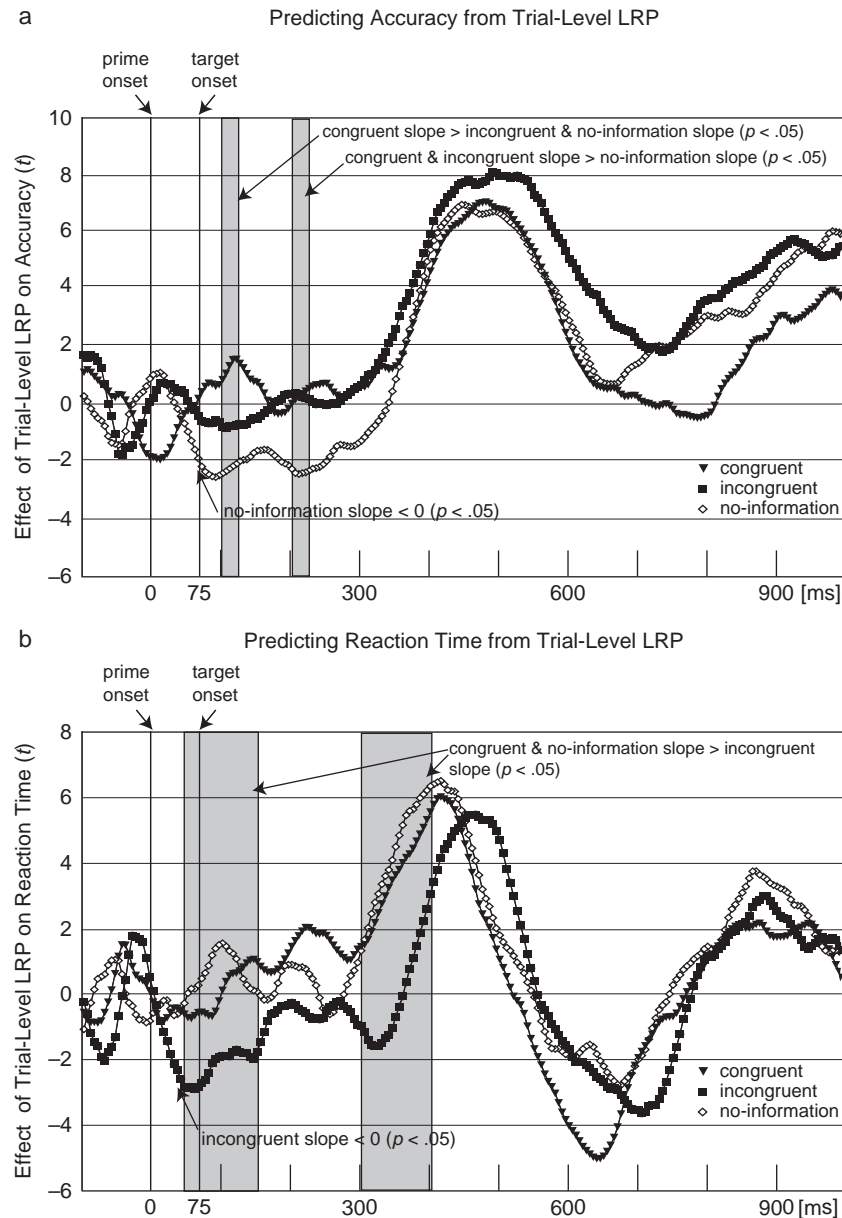
Figure 3. The effect of trial-level covert motor activation (TCMA) on (a) accuracy and (b) response times for correctly classified targets, as a function of trial type (congruent, incongruent, and no-information). *T* values correspond to the level-2 estimate (γ_{10}), representing the average effect of TCMA on behavioral performance. *T* values are plotted across time post prime onset. A positive *t* value, reflecting a positive slope, indicates that covert motor activation associated with the correct (vs. incorrect) response predicted better (more accurate, faster) behavioral performance. A negative *t* value reflects a negative slope and indicates that covert motor activation associated with the correct (vs. incorrect) response predicted worse (less accurate, slower) behavioral performance. TCMA was computed by taking, for each trial, the difference between potentials at C3 minus potentials at C4, multiplying these differences by -1 for trials in which the target cued the left-hand, and averaging across 60-ms intervals that were shifted by 5 ms (220–279 ms, 225–284 ms, etc.). Each time interval of the trial-level LRP is referred to by its midpoint. Thus, in the figure above, the point associated with trial-level LRP at 220 ms corresponds to covert motor activation occurring between 190–249 ms.

no-information trials, on the one hand, and congruent and incongruent trials, on the other. Starting as early as 70 ms post prime onset, greater covert motor activations of the correct response predicted decreased accuracy on no-information trials, and no such pattern emerged on congruent and incongruent trials. Thus, whereas analyses of the subject-level grand-averaged LRPs indicated that the mean level of activation on no-information trials did not differ from zero until 340 ms post prime onset (see Figure 2a), the trial-level analyses indicated that the

variability of covert motor activations, which is centered around zero, is in fact meaningful.

Furthermore, at approximately 105 ms post prime onset, trial-level covert motor activations of the correct response predicted greater accuracy on congruent trials than incongruent and no-information trials. These trial-level effects were observed even though analyses of the subject-level, grand-averaged LRPs indicated no significant covert motor activation during the same period of time (i.e., the grand-averaged LRP

on congruent trials at approximately 105 ms did not differ significantly from zero).

Finally, as time post prime onset elapsed (>300 ms post prime onset), trial-level covert motor activations of the correct response significantly predicted higher accuracy for all trial types. The onsets of these later occurring trial-level effects were 365 ms, 365 ms, and 340 ms for congruent, no-information, and incongruent trials, respectively. These onsets correspond approximately with the onsets for the grand-averaged LRPs (Figure 2a).

Predicting reaction times from trial-level covert motor activations. The same MLM strategy (see *MLM Analyses of TCMA Effects* in the *Method* section) was used to predict RT on correctly classified trials. Figure 3b plots the *t* values corresponding to γ_{10}, and reflects the predictive ability of each 60-ms TCMA interval over time for each trial type separately. A positive *t* value indicates that greater covert motor activations of the correct (vs. incorrect) response predicted faster RTs. A negative *t* value indicates that greater covert motor activations of the correct response predicted slower RTs.

A noticeable effect is the difference in predictive ability between incongruent trials, on the one hand, and congruent and no-information trials, on the other. Starting at 30 ms post prime onset, trial-level covert motor activations of the correct response was associated with slower RTs on incongruent trials. This pattern was not observed on congruent and no-information trials. Thus, even though analyses of the grand-averaged LRPs indicated no significant covert motor activation during the same period of time, the MLM analyses showed that variability in covert motor activations on incongruent trials significantly predicted RTs in classifying targets.

In addition, as time post prime onset elapsed (>300 ms post prime onset), trial-level covert motor activations of the correct response predicted faster RTs for all trial types. The onsets of these effects were 320 ms for congruent and 310 ms for no-information trials and delayed by 70–80 ms on incongruent trials (390 ms). They also correspond approximately with the onsets for the grand-averaged LRPs (Figure 2b).

Discussion

Behavioral Priming Effects

Analyses of behavioral responses showed that primes facilitated, as well as hindered, subsequent behavioral performance on the target classification task. Specifically, on trials in which the gender of the prime matched the gender of the target (congruent), classification of targets was both more accurate and faster, compared to trials in which primes provided no information about gender. Conversely, on trials in which the gender of the prime was opposite of the gender of the target (incongruent), classification of targets was both less accurate and slower, compared to trials with no-information primes. Thus, even though participants were instructed to classify targets and ignore primes, primes affected the ease with which participants were able to perform the subsequent target classification task.

Evidence of Prime-Induced Covert Motor Activations: Grand-Averaged LRPs

Results from the standard subject-level analyses of the grand-averaged LRPs showed that masked primes triggered preparatory covert motor activations, consistent with past findings (Dehaene et al., 1998). Support for this claim is based on two findings: the initial direction of the LRP for congruent and incongruent trials

and the delayed LRP onset for no-information trials. As shown in Figure 2a, the LRP for congruent trials was initially negative (upward going), indicating greater covert preparatory motor activations of the correct target response. In contrast, the LRP for incongruent trials was initially positive (downward going), indicating greater preparatory motor activations of the incorrect target response. Moreover, compared to congruent and incongruent trials, the LRP onset for no-information trials was delayed by approximately 70 ms, which is approximately the same time interval by which targets followed primes.

It is worth noting that in the present experiment prime-induced covert motor activations persisted long enough to overlap with motor activations triggered as a response to the target. Specifically, the time interval in which the LRP onset for no-information trials became statistically significant is assumed to reflect the onset of activation triggered primarily by the target. During this time interval, congruent trials showed greater covert activations of the correct response, whereas incongruent trials showed greater covert activations of the incorrect response.

Evidence of Spontaneous Covert Motor Activations: Multilevel Analyses of Covert Motor Activations on Performance

Subject-level analyses do not unequivocally establish that preparatory covert motor activations, indexed by the LRP, and subsequent behavioral performance (accuracy, RT) occur in known sequence on individual trials. In contrast, MLM is appropriate for estimating trial-level effects of covert motor activations on subsequent behavioral performance, how these covert motor activations interact and depend on incoming information, as well as the strength of these effects over time.

In some respects, the results from the MLM converged with the results from the grand-averaged LRP analyses. Specifically, MLM analyses revealed that for the three trial types covert motor activations of the correct response occurring approximately 300–400 ms post prime onset was associated with enhanced behavioral performance, as indexed by higher accuracy (Figure 3a) and faster RTs (Figure 3b).

However, most important, the findings from the MLM analyses provide information that goes beyond the analyses of the grand-averaged LRP waveforms. With regard to the later occurring trial-level effects (>300 ms post prime onset), the MLM analyses indicate that *within* each trial type, spontaneous activations of the correct response predicted higher accuracy and faster RT. Whereas analyses of the grand-averaged LRPs focus on differences in covert motor activations between the trial types (e.g., activation of the correct response occurs earlier for congruent than no-information trials), the MLM analyses focus on within trial type variation. The results of MLM show that, even when controlling for differences across trial types, covert motor activation predicted accuracy and RT. To provide a more concrete illustration, grand-averaged LRPs showed an earlier onset of covert motor activations of the correct response on congruent trials (compared to no-information and incongruent trials). The trial-level analyses show that, among congruent trials, spontaneous covert motor activations of the correct response, occurring approximately 300–400 ms post prime onset, predicted faster reaction times and greater accuracy on the target classification task. Although past work (Gratton et al., 1988) has shown that prestimulus covert motor activations predict responses on "fast guess" trials in which responses occur within 150–199 ms, the present findings indicate that within trial variation of covert motor activations predicts responses on trials with longer RTs as well.

Moreover, the MLM analyses also revealed that fluctuations in covert motor activations early on in the stimulus stream (<150 ms post prime onset) interacted with, and depended on, the prime information encountered. As illustrated in Figure 3a, if early in the stimulus stream (<150 ms post prime onset), the motor circuits associated with the correct response were activated, (a) encountering a congruent prime was associated with increased accuracy in classifying the target, (b) encountering a no-information prime, which is not relevant to the target classification task, was associated with decreased accuracy, and (c) encountering an incongruent prime was relatively unassociated with subsequent accuracy. The findings that spontaneous covert motor activations interacted with prime information suggest a variant of response competition processes. More concretely, if covert motor activations occurring early in the stimulus stream are followed by information (primes) that reinforces the initial activations, then the initial activations are further enhanced. If covert motor activations are followed by information that is not consistent with, or opposite of, the initial activation, then the initial activation may not be enhanced, and may even be inhibited. These findings are consistent with models of human information processing that emphasize the partial accumulation of evidence over time (e.g., Osman et al., 1992) as well as models assuming continuous (versus discrete or all-or-none) patterns of response activations underlying overt behavioral responses and decision-making (e.g., Coles et al., 1985; Dale, Kehoe, & Spivey, 2007; Eriksen & Schultz, 1979; Eriksen, Coles, Morris, & O'Hara, 1985; McKinstry, Dale, & Spivey, 2008; Nosofsky & Palmeri, 1997).

Most important, the findings of spontaneous fluctuations in covert motor activation occurring <150 ms post prime onset influencing later behavioral responses are not observed in the grand-averaged LRP waveforms (Figure 2a). That is, whereas the analyses of the aggregate subject-level grand-averaged LRP indicate that covert motor activations were not significantly different from zero in the period <150 ms post prime onset, the trial-level covert motor activations, indexed by TCMA, indicate that variation in the activity is meaningful and influential.

Further, highlighting the utility of applying MLM to complement the grand-average analyses, the MLM analyses, but not analyses of the grand-averaged LRPs, provide information about the role of covert motor activations in the behavioral priming effects observed in the RTs for correctly classified trials. Specifically, on correctly classified trials, priming effects emerged in RTs (i.e., slower RTs on incongruent than congruent and no-information trials; see Table 1). Results from the MLM analyses suggest that covert motor activations may be playing a role in the slowing of RT for incongruent trials. As shown in Figure 3b, on incongruent trials, starting at 30 ms post prime onset, greater covert activations of the correct response predicted longer RTs. This suggests that, if early in the stimulus stream covert motor activations favor the correct target response, encountering incongruent information (prime) may inhibit these initial activations, leading to slower RTs in classifying targets. Most important, analyses of the grand-averaged LRPs for correctly classified incongruent trials did not reliably show activations of the incorrect response (i.e., at no point was the LRP significantly different from zero in the positive direction; Figure 2b).

Outstanding Questions and Future Directions
It is noteworthy that early (<150 ms post prime onset) trial-level covert motor fluctuations were differentially related to accuracy and RTs. For example, on incongruent trials, covert motor ac-

tivations occurring early in the stimulus stream were relatively unassociated with subsequent accuracy (Figure 3a), but were negatively associated with RTs (Figure 3b). On no-information trials, early covert motor activations were inversely associated with accuracy (Figure 3a), but were not reliably associated with RTs (Figure 3b). Finally, on congruent trials, early covert motor activations (starting at 70 ms post prime onset) were related to greater accuracy (Figure 3a), but were not significantly related to RTs (Figure 3b). The source of these dissociations observed in the early occurring (<150 ms post prime onset) trial-level effects is unclear. One speculation based on observations of dissociations between reaction times and accuracy observed in other tasks, such as letter recognition (Santee & Egeth, 1982) and spatial cueing tasks (Prinzmetal, McCool, & Park, 2005), is that different neural and cognitive mechanisms operate at different stages of conflict resolution (Casey, Thomas, Welsh, Badgaiyan, Eccard, Jennings, & Crone, 2000).

Moreover, a central aim of the present research was to investigate the role of spontaneous covert motor activations on subsequent behavioral responding. Although spontaneous covert motor activations were defined in the present experiment as covert motor activations not driven by an external stimulus (i.e., prime) and appearing to be more or less random, a valuable next step is to assess whether these variations may be predicted by the preceding response or expectations about the upcoming target. Nonetheless, irrespective of the sources influencing spontaneous fluctuations, we believe that their ability to predict subsequent behavior (accuracy and RT) and interactions with prime information are likely to extend to other tasks. Another promising avenue for future work is to assess the generalizability of these findings to other paradigms.

As a final point, the present experiment shows that trial-level motor activations, both those occurring late in the stimulus stream (>300 ms post prime onset) as well as early in the stimulus stream (<150 ms post prime onset), are associated with the ease with which the target classification is performed. It is possible that the response window procedure used in the present experiment, which obliged participants to respond more rapidly than they would naturally be inclined to do, predisposes participants to use any cues, external and internal, available to them for making the target classification judgment within the response window. As such, participants may increase their reliance on not only the prime information (external cue), but also on differential levels of covert motor activation that predispose one motor movement over another (internal cue). Although we believe that the effects observed in the present research reflect a more general phenomenon—that is, that fluctuations in covert motor activations influence the processing of incoming stimuli as well as subsequent behavioral response—future research is needed to establish whether such effects would be reliably observed using priming paradigms that do not employ a response window.

Conclusions

This research is the first to apply MLM statistical techniques to electrophysiological data to establish the role of unintentional covert motor activations on subsequent behavior. The trial-level analyses indicated that spontaneous covert motor activations (>300 ms post prime onset) of the correct response occur to a greater extent on trials in which targets are correctly classified, as well as on trials in which targets are classified more quickly.

Moreover, the present work identifies that early occurring spontaneous fluctuations in covert motor activations are a source of influence on behavioral performance. Trial-level analyses revealed that early (< 150 ms post prime onset) covert motor activations interacted with, and depended on, prime information to predict subsequent accuracy and reaction times. Critically, these findings of spontaneous covert motor fluctuations would be otherwise unobserved with standard subject-level, multitrial-aggregation analyses.

The present findings are consistent with models assuming continuous (versus discrete or all-or-none) patterns of response activations underlying overt behavioral responses and decision-making (e.g., Coles et al., 1985; Dale et al., 2007; Eriksen & Schultz, 1979; Eriksen et al., 1985). Moreover, whereas past research has focused on how sensory information affects the motor system without conscious awareness, the present findings suggest that covert motor activations may impact the processing and effect of initial perceptual information.

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