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Varieties of action control: Event-related brain potentials of responding to symbolically congruent and incongruent cues

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Abstract

Performing infrequently enacted responses requires overcoming a competing tendency to perform prepotent, frequently enacted responses. Similarly, responding to symbolically incompatible cues requires overcoming a competing tendency to perform prepotent, cue-compatible responses. To examine neural correlates of these aspects of human self-regulation, event-related brain potentials were acquired in two separate modified oddball experiments in which participants responded to all stimuli. Stimuli varied in frequency and in compatibility with the participants' intended actions. Irrespective of stimulus–response-compatibility, low-frequency responses were associated with P3 event-related potentials (ERPs) of maximal amplitude at posterior electrode sites. In contrast, irrespective of stimulus–response frequency, stimulus-incompatible responses were associated with enhanced P3 mean amplitude at frontal electrode sites. This prefrontal positivity was not affected by whether participants' actions were predetermined (always responding in single direction) or rule determined. Taken together, the findings indicate that response-compatibility effects are distributed in brain regions that overlap and extend beyond response frequency neural networks. © 2007 Elsevier Inc. All rights reserved.

Keywords: Action control; ERPs; Event-related potentials; P300; P3; Amplitude; Response-selection; Response-compatible

1. Introduction

Goal-directed action requires behaving consistently in varying contexts. Indeed, self-control often is defined as acting according to rules or intentions despite the presence of conflicting situational information [1,2]. Accordingly, understanding how people map intended actions onto incompatible cues has been a major focus of diverse research efforts [3–7]. Whether grounded in behavioral findings [8,9], electrophysiological findings [10,11], or functional imaging findings [12], emerging from these efforts is a fundamental question: to what extent does a general, unitary mechanism handle different types of conflicts between intended actions and contextual cues?

Recent computational and neuroimaging work has emphasized stimulus-response frequency as a general determinant of action conflict, mediated by structures in the anterior cingulate cortex and its connections with networks that underlie a wide range of executive functions [13-17]. Frequency of performance of a particular response strongly influences response conflict, in that "for the low-frequency response to be executed, it must compete with and eventually overcome the bias toward producing the prepotent [high-frequency] response tendency" [[14], p. 17]. This perspective has helped explain several classically studied effects. Electrophysiological evidence [14] and functional imaging evidence [13,18] have implicated a unitary neural mechanism underlying human performance in the oddball experimental paradigm (in which participants actively respond to certain rarely occurring stimuli) and the go/no-go experimental paradigm (in which participants withhold active responses to certain rarely occurring stimuli). In both cases, a presumed conflict between highly accessible (high-frequency) intention-incompatible responses and less accessible (low-frequency) intention-

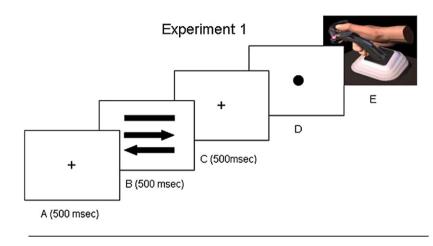
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compatible responses is presumed to recruit a general-purpose conflict-detecting mechanism.

The present research probed the generality of the frequencybased account of action–context conflicts. More specifically, in two independent studies, we examined frequency-based effects and effects of action–context conflict as instantiated in stimulus– response (S–R) compatibility. Beginning with the work of John Ridley Stroop [7] and continuing throughout extensive research programs [for a review see, [19]], research on S–R compatibility has exploited human subjects' highly over-learned responses to symbolic stimuli, helping elucidate how people handle action– cue conflicts, such as following an intention of moving to the right upon viewing a left-pointing arrow.

The present research builds on a long tradition of neurophysiological work on the P3, an endogenous, late-positive component often elicited by low-frequency events [[20], for review see, [21]]. The P3 has proved over the last several decades to be an extremely robust neural correlate of stimulus–response frequency, reliably elicited, for example, when people need to perform particular actions in response to low-frequency cues (rather than performing other actions in response to high-frequency cues) [22]. Numerous studies have furthermore demonstrated a useful distinction among types of P3 components based on anterior (frontal) versus posterior (parietal) distribution patterns, hence increasing the specificity of this neural marker [4,23,24]. McCarthy and Donchin [6] assessed effects of stimulus-classification difficulty and response-compatibility on P3 latency. Whereas P3 latency was affected by the ease of stimulus classification, it was independent of response-compatibility/incompatibility (For similar effects, see [26–29]). Given emphases on mental chronometry, and given early limitations on the density of electrode placement, however, much of response-compatibility research has focused on P3 latency rather than on P3 spatial distribution. More recent work has begun to suggest important effects of S–R compatibility on fluctuations in P3 amplitude [33] as well as latency [30].



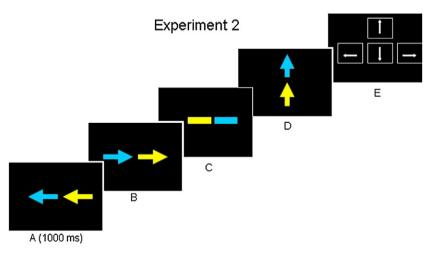


Fig. 1. Experiment 1. Following fixation point (A), one of the three stimuli in (B) appeared, with left and right arrows each occurring with .1 probability and horizontal bars occurring with .8 probability. A second fixation period followed stimulus presentation. A dot (D) cued joystick responses (E), in which participants pressed the top button for horizontal bars and move the joystick in a single, predefine direction (left or right, counterbalanced across participants) for both arrows. Experiment 2. Stimuli consisted of three stimulus types: response-compatible (p=.125), response-incompatible (p=.125), and response-neutral (p=75). Participants were instructed that their task was to respond to pairs of arrows or rectangles using the keyboard arrow keys. They were required to press the arrow key in location of BLUE arrows (or the yellow arrows, counterbalanced across participants). Compatible trials (i.e., A, D) entailed responding to the location of the target color when the arrows coincidentally pointed in the opposite direction of one's response. Neutral trials (i.e., C) entailed pressing the spacebar.

In light of these past findings, we explored whether or not frequency-based neurophysiological responses varied as a function of S–R compatibility. This issue was tested in two independent modified oddball tasks where participants' responses were either predetermined or rule-related determined. We hypothesized that if low-frequency compatible and incompatible cues involve identical processes, then, the ERP patterns will be similar irrespective of compatibility. In contrast, if mechanisms that underlie compatible and incompatible processes differ in strength or neural generators, then the ERP waveforms will differ in their characteristics.

2. Method

2.1. Participants

Ten right-handed individuals (seven males), between the ages of 18 and 31, participated in Experiment 1. In Experiment 2, 17 right-handed individuals (nine males), between the ages of 18 and 24, participated. Data from five participants in experiment 2 were excluded from the analysis due to an excessive number of trials contaminated by artifacts. All participants had normal or corrected-to-normal vision and received course credits or cash compensation (\$15 per hour) for participation.

2.2. Procedure

Both experiments were conducted in a dimly lit soundattenuating chamber, with participants seated comfortably in a reclining chair. Stimuli were presented via a 15 inch computer monitor, which was centered one foot from the participant. The experimenter provided instructions to remain still, and, when possible, to refrain from blinking.

2.2.1. Experiment 1

Stimuli consisted of three different images: a left-pointing arrow (p=.10), a right-pointing arrow (p=.10), and a horizontal bar (p=.80). A joystick mounted on a lap-board was used for responding (Fig. 1). The instructions were to press the button atop the joystick whenever a horizontal bar was presented and to move the joystick always in the same direction (either left or right, counterbalanced across participants), for any arrow stimuli. An experimental trial consisted of a 500ms fixation, followed by a stimulus (left arrow, right arrow, or horizontal bar) that remained for 500ms Next, a 500ms fixation appeared again. Lastly, a dot appeared, cuing the response. The 500ms delay between presentation of the critical stimuli (i.e., the arrows) and the final cue (the dot) was included to allow for evoked potential recordings free from motor contamination, given that the required response, moving a joystick, has not often been studied in ERP studies and plausibly could increase error in electrophysiological measurement. In this regard, it is important to note two points. First, ERP epochs reported below were linked to presentation of the critical stimulus (e.g., the arrow stimuli), not to the dot that followed. Second, we conducted a behavioral pilot study (with 10 participants) using the same procedures detailed above, except that participants made their responses as soon as the critical

stimuli (e.g., the arrows) appeared. In the pilot study, participants required an average of 530.09ms to respond to the frequent stimulus, 714.76ms to respond to the compatible/infrequent stimulus, and 780.66ms to respond to the incompatible/infrequent stimulus. The 65.90ms (SD=32.36ms) S-R compatibility effect (i.e., Incompatible RT minus Compatible RT) was statistically significant, t(9) = 6.44, p < .001, and the 217.62ms (SD=78.11ms) oddball effect (i.e., average Incompatible/Infrequent plus Compatible/Infrequent RT minus Frequent RT) also was statistically significant, t(9)=8.81, p<.0001. Data from the pilot study thus confirm that the present stimuli and design successfully impact behavior as a function of stimulus-responsecompatibility and response frequency. In the ERP experiment, response accuracy was stressed, and all participants indeed achieved greater than 95% accuracy. An error message was displayed for 500ms for any incorrect responses. The experiment consisted of two blocks, each with 150 trials. Participants were provided a threeminute rest between blocks.

2.2.2. Experiment 2

The design and stimuli were as described in Experiment 1, with the exceptions that (a) only the task-irrelevant cues were used; (b) the proportion of compatible to incompatible arrow stimuli was .50 for all participants; (c) the overall number of trials (600) was precisely twice as many as in Experiment 1 (which had 300); (d) all stimuli remained visible for a 1000ms period, after which trials ended automatically; and (e) on 75% of trials, rectangles, rather than arrows, were presented. The

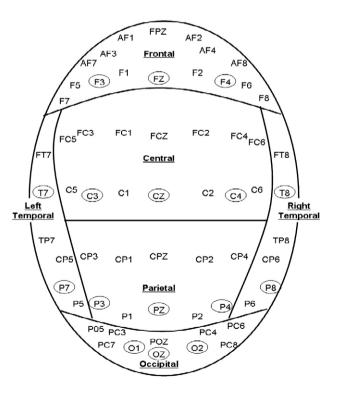


Fig. 2. Layout of the electrode array used for statistical analyses. There were six regions examined in each study. In experiment 1 (64-channel electrode cap), the electrodes in the whole regions were analyzed. In experiment 2 (21-channel electrode cap) the circled electrodes were used.

Table 1 Average response times (in milliseconds) and proportions of correct responses from Experiment 2

Stimulus	Response time	Proportion correct
Incompatible ($p=.125$)	583.66 (64.86)	.91 (.07)
Compatible ($p=.125$)	520.79 (47.80)	.95 (.06)
Neutral $(p=.75)$	374.97 (40.00)	.99 (.02)

rectangles were presented in pairs, oriented the same way as the arrows (i.e., horizontally or vertically, with equivalent probability), and colored the same way as the arrows (i.e., one in solid light blue, the other in solid yellow, with all combinations equally probable). Using a standard keyboard, participants' were instructed to use the arrow keys to respond to the arrows (by pressing arrow key corresponding to location of the blue arrows or the yellow arrows, counterbalanced across participants) and to press the spacebar whenever rectangle stimuli appeared (Fig. 1). Accordingly, frequent trials entailed pressing the spacebar. Compatible trials entailed responding to the location of the target color when the arrows coincidentally pointed in the same direction as one's response, whereas incompatible trials entailed responding to the location of the target color when the arrows coincidentally pointed in the opposite direction of one's response.

2.3. ERP recordings

Experiment 1 EEG was recorded continuously using a 64channel (Neuroscan Inc., Sterling USA), and Experiment 2 EEG was recorded using a 21-channel (Electro-Cap) electrode cap systems. All recordings were performed using a frontocentral electrode as ground, and electronically-linked mastoid electrodes as reference. The horizontal EOG was monitored from electrodes at the outer canthi of the eyes, and the vertical EOG was monitored from electrodes above and below the orbital region of the left eye. Impedances for all electrodes were kept below 10k Ω . The EEG and EOG signals were digitized at 1000Hz, and were amplified with a gain of 500. The filter bandpass was .01–30Hz. To eliminate EOG artifact, trials with EEG voltages exceeding +/–100µV were rejected from the average. Artifact rejection and averaging were done off-line. Approximately 20% of the trials were excluded due to artifacts.

2.3.1. Data analysis

EEG epochs began 100ms prior to stimulus onset and continued for 900ms after stimulus onset. Independent averages were generated off-line for compatible-infrequent, incompatible-infrequent, and neutral-frequent stimulus types. Grand averages of ERP waveforms for each stimulus type were constructed for illustrative purposes and for determination of P3 amplitude measurement. ERPs were quantified by measuring the mean amplitude in the 250 - 550ms latency window. To simplify the analyses and presentation of the scalp distribution findings, electrodes were grouped into six regions: Frontal, Central, Parietal, Left Temporal, Right Temporal, and parietal-Occipital. In the advent of a malfunctioning electrode, the amplitude was substituted by the group-mean. The layout of electrodes used for Experiment 1 and 2 is presented in Fig. 2. To reduce the likelihood of Type I errors, the Greenhouse-Geisser correction was used for all comparisons with more than two within-subject levels.

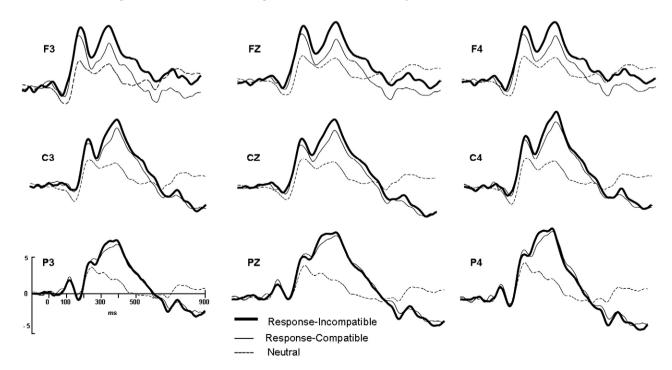


Fig. 3. Grand average ERP waveforms from Experiment 1 superimposed for each stimulus type: response-compatible, response-incompatible, and neutral stimuli types. The data are shown for nine electrode locations at left (F3, C3, P3), midline (FZ, CZ, PZ), and right hemisphere (F4, C4, P4) sites over anterior (F3, FZ, F4), Central (C3, CZ, C4), and posterior (P3, PZ, P4).

3. Results

Participants' response times acquired from Experiment 1 were not time-locked to stimuli (withheld response until the onset of cue stimulus) and were not analyzed. Table 1 shows the mean response time and percentage of correct responses for each of the three stimulus types from Experiment 2. One-way repeatedmeasure ANOVA revealed response times differed significantly across stimulus types, F(2, 22)=11.23, p<.04. Most relevant to our investigation, and supporting that we successfully manipulated response-compatibility versus incompatibility, participants responded much more slowly (difference M=62.87ms, SD=35.18) to incompatible than to compatibles stimuli, t(12)=6.19, p<.0001. Performance accuracy was greater than 90% for all stimulus type, with fewer errors obtained for compatible and neutral than incompatible stimuli.

3.1. ERP waveforms

Fig. 3 shows grand average ERP waveforms for each stimulus type from Experiment 1. As expected, irrespective of response-compatibility, infrequent stimuli elicited an enhanced late-positive component maximal at central-parietal electrode

for response-incompatible than for response-compatible stimuli. Data from Experiment 1 and 2 were analyzed separately in 3 (Stimulus Type)×6 (Electrode Region) within-subjects ANO-VAs. Experiment 1 analyses indicated significant main effects of Stimulus Type [F(2, 18)=27.98, p<.001] and of Electrode Region [F(5, 45) = 19.44, p < .02] and a significant interaction between the two factors, [F(10, 90)=5.00, p<.001]. To examine differences in the topographical distribution of response-compatibility effects, we computed mean amplitude difference by electrode region. The analysis of scalp distribution revealed that mean amplitude differences between response-compatible versus response-incompatible were significant at the frontal region [difference $M=2.34\mu$ V, SD=2.70, t[10]=2.74, p<.05) and the central region [difference $M=1.49\mu$ V, SD=1.86, t[10]=2.54, p < .05) but not at any other regions. The corresponding Experiment 2 analyses similarly indicated significant main effects of Stimulus Type [F(2, 22)=14.75, p<.001] and of Electrode Region [F(5, 55)=10.29, p<.001] and a significant interaction

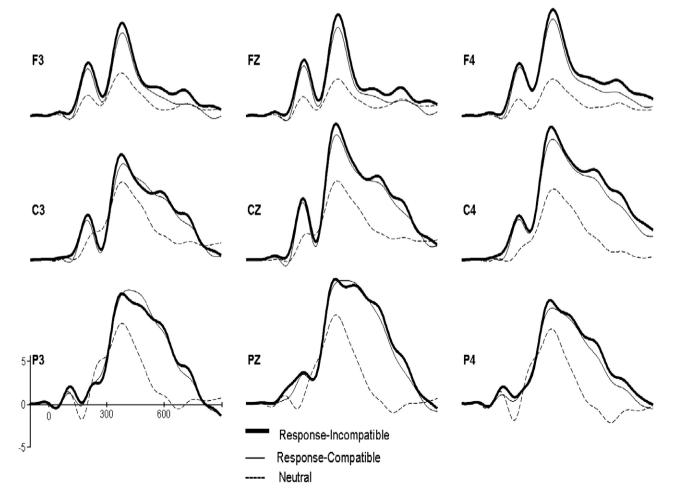


Fig. 4. Grand average ERP waveforms from Experiment 2 superimposed for each stimulus type: response-compatible, response-incompatible, and neutral stimuli types.

between the two factors, [F(10, 110)=5.93, p<.001]. Results further revealed that P3 mean amplitude differences were significant at frontal [difference $M=.87\mu$ V, SD=1.25, t(12)=2.42, p<.05] but not at any other regions. Comparisons of mean P3 amplitudes during responses to common (horizontal bar) and the combination of both types of rare (compatible and incompatible arrows) stimuli served as a measure of the frequency-based oddball effect. In both experiments, when collapsing across the two levels of response-compatibility, infrequent stimuli were associated with enhanced P3 mean amplitude at all electrode regions (p<0.05).

4. Discussion

The present results show converging evidence from two experiments in support of the notion that frequency-based and response-compatibility-based conflicts can be dissociated by means of P3 scalp topography. Irrespective of compatibility, low-frequency stimuli elicited parietal P3s there were identical in amplitude. In contrast, stimulus-incompatible responses were associated with greater frontal positivity than stimulus-compatible responses. Rather than a unitary, general brain mechanism handling these different types of conflict between intended actions and contextual cues, more specialized mechanisms appear to be engaged by the respective challenges of executing low- vs. high-frequency responses, and cue-incompatible vs. cue-compatible responses.

An important question, however, is why stimulus-incompatible responses elicited greater frontal positivity than stimuluscompatible responses. This anterior effect may result either from a stronger activation of the same generator(s) or reflect the activation of other brain regions that contribute to overcoming prepotent and incompatible responses. Functional neuroimaging studies support that specific brain structures, most notably the dorsal anterior cingulate cortex (ACC), play an important role in response-selection as well as detecting and resolving conflict [12,18,31,32]. Accordingly, conflict is magnified when a task-irrelevant feature (direction of cue stimulus) is associated with a response that is incongruent with the response associated with the task-relevant information. One limitation of scalp recordings is that the underlying neural generators cannot be identified and inference is limited to time sequences of waves varying in magnitude and topography. Although the present results cannot directly link the neural signals distributed in the frontal regions to brain structures implicated in the functional imaging studies, we hypothesize a similar mechanism of action and greater cognitive effort in overcoming incompatible relative to compatible responses. The results further characterize that the differences were unaffected whether participants' actions were predetermined (always responding in single direction) or rulerelated determined.

Consistent with behavioral results from previous studies [19], results from Experiment 2 showed that participants respond more slowly to response-incompatible than to response-compatible stimuli, presumably reflecting biasing tendencies to respond to symbolic stimuli in a symbol-consistent manner. Research further supports that people respond more slowly to infrequently occurring cues than to frequently occurring cues, presumably reflecting biasing tendencies to perform highly accessible (through frequency of usage) responses [13]. Given this basic commonality of overcoming a prepotent response to execute a less accessible one, what accounts for the presently observed behavioral differences associated with generating low-frequency and cue-incompatible responses? One important difference between these two phenomena is that only S-R compatibility conflicts involve the presentation of new, response-conflicting information precisely at the moment of response generation. Frequency-based effects on action-context conflicts, in contrast, appear to reflect an accumulating preponderance in episodic memory of instances of generating a particular type of response (the highly frequent one) [1]. This fundamental difference, then, of acute need for self-control in response to a particular incompatible cue, versus a broader-based need for self-control in response to accumulating bias to perform a particular response, may help explain our findings that different brain mechanisms apparently underlie these two central aspects of human self-regulation.

Christensen and colleagues (2001) observed higher-amplitude late-positive ERPs to incompatible than to compatible cues [33]. Importantly, however, those effects emerged quite late, beginning around 600ms after stimulus presentation. Accordingly, the authors interpreted their findings as related to a distinct, later potential, dubbed "P4," and they suggested a functional distinction between the P3 and P4, only the latter of which was argued to play a role in response-selection. Our findings, in contrast, point to clear stimulus-response-compatibility-based differences in amplitude (again with higheramplitude for incompatible than compatible responses) much earlier, beginning around 300ms following stimulus presentation. Two key design features in our experiment may account for this divergence. First, the stimuli in the present study consisted of visual symbols while those used in Christensen et al. (2001) study were words, and specialized neural circuits that underlie word versus symbolic evaluation may contributed to these differences. Symbolic objects are processed faster reflected in shorter response times and P3 latencies than the same objects presented as words [25]. Second, participants in Christensen et al. study (2001) received instructions emphasizing speedaccuracy performance. Although we stressed on the importance of accuracy, we did not monitor for speed versus accurate tradeoff, and strategic differences utilized within-subjects may have masked processing differences that are reflected in P3 and P4 components.

Previous investigations of the effect of response-compatibility on P3 latency have yielded mixed findings, with some studies reporting that P3 latency reflects stimulus evaluation but not response-selection [6,28], and other studies that show P3 latency is sensitive to stimulus evaluation as well as responseselection [29,34]. An alternative hypothesis is that P3 latency is sensitive to both stimulus and response-related processing when response time is fast, and decreases with factors that increase response time [35].

As illustrated in Figs. 2 and 3 (confirmed in an unreported analysis), the P3 latencies for response-compatible and incompatible stimuli were almost identical. Nonetheless, processing time for incompatible stimuli were longer, supporting that compatibility was successfully manipulated but had no effect on P3 latency. Therefore, the present results favor the view that the P3 latency reflects stimulus evaluation but not response-selection.

A major limitation of this study expressed by one of the referees was that response and stimulus types were affected with frequency. It is likely that the brain potentials were mediated with stimulus processing rather than overcoming prepotent responses. We agree that waveforms are contaminated with factors that extend beyond the experimental variables; however, we examined a specific component of the event-related waveform that is selective to task-relevance and stimulus probability. Nevertheless, a design that encompassed response-compatible (.10), response-incompatible (.10), response-neutral (.10), and distractors (.70) would have allowed a rigorous comparison among all these factors. This is an intriguing question and a potential experiment in a subsequent study.

We sought to identify the event-related brain potentials that underlie overcoming prepotent stimuli and responding to symbolically incompatible and compatible cues. The results revealed that irrespective of frequency, response-incompatible cues were associated with greater P3 amplitude at frontal electrode sites than response-compatible cues. The study highlights the usefulness of P3 amplitude and frontal–parietal topographical distribution in human goal-directed action control.

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