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Voluntary Stimulus Production Enhances Deviance Processing in the Brain

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Abstract

Humans often get information by voluntary action. However, little is known about how stimulus processing is modulated by self-production of stimuli. In the present study, event-related brain potentials were recorded from sixteen student volunteers performing an auditory three-stimulus oddball task in two conditions. In the self condition, the stimuli were triggered by participants' voluntary button presses. In the auto condition, the same stimuli were presented automatically by a computer with the same interstimulus intervals as those in the self condition. Perceptually deviant nontarget stimuli elicited a larger P3 and a larger subsequent positivity in the self condition than in the auto condition, whereas low-deviant target stimuli elicited a P3 with equally high amplitude in both conditions. The findings suggest that voluntary stimulus production enhances orienting of attention (reflected in the P3a component) and subsequent memory updating (reflected in the P3b component) for deviant stimuli, but does not affect the response to task-relevant stimuli. Voluntary action may activate the perceptual representation of its most frequent outcomes and this anticipatory activation may make deviant stimuli more salient in the context.

Keywords: event-related potential, voluntary action, action effect, orienting response, P3a, P3b

1. Introduction

Knowledge about stimulus processing and attention in humans has been acquired mainly from experiments in which participants are asked to keep still and wait for stimuli to be presented at an externally determined pace. In everyday life, however, humans often get information by voluntary action. Although the significance of recording brain activity during this "interactive" situation has been suggested by several researchers (O'Connor, 1981; Papakostopoulos, 1980; Schafer and Marcus, 1973), few studies have examined how stimulus processing is modulated by voluntary production of stimuli.

Previous studies using event-related brain potentials (ERPs) have shown that the P3 (P300) wave recorded in a simple target detection (oddball) task is sensitive to voluntary stimulus production. McCarthy and Donchin (1976) used a two-tone oddball task in which participants counted 1500 Hz tones ($p = .10$) embedded in a sequence of 1000 Hz tones ($p = .90$). They found that the amplitude of the P3 elicited by rare target tones increased at the vertex (Cz) when the tones were presented immediately after participants' button presses, compared to when the tones were presented automatically without button presses. This finding was replicated and extended by Nittono and Ullsperger (2000), who used a novelty oddball task in which participants responded to 2000 Hz target tones ($p = .10$) embedded in a sequence of 1000 Hz standard tones ($p = .80$) and task-irrelevant, computer-edited novel sounds ($p = .10$). Target stimuli elicited a centroparietal P3, whereas novel stimuli elicited a frontocentral P3.

When the stimuli were triggered by voluntary button presses, both P3s increased in amplitude particularly at frontocentral sites. Nittono et al. (2003) obtained similar results in the visual modality. Participants were asked to count one of the infrequent stimulus categories among three alphabetic letters (S, H, and O) presented with probabilities of .125, .125, and .750. When the stimuli were triggered by participants, the amplitude of an early part of the P3 wave (350–445 ms) to both target and nontarget rare stimuli increased at frontocentral sites. Since the amplitude increase did not occur for frequent stimuli, the P3 enhancement was not due to the overlap of movement-related potentials associated with self-triggering. Finally, Nittono (2004) replicated a central dominant increase of the P3 for self-produced infrequent target stimuli in both auditory and visual modalities using a typical two-stimulus oddball task.

The scalp-recorded P3 wave has been assumed to consist of at least two different but mutually related components, P3a (or novelty P3) and P3b (Courchesne et al., 1975; Squires et al., 1975). The P3a has a shorter peak latency than does the P3b and is distributed more anteriorly than the P3b, reflecting the involvement of different neural generators (Halgren et al., 1998; Knight and Scabini, 1998). The P3a is sensitive to contextual salience (or novelty) of the eliciting stimulus, and is assumed to be a manifestation of the frontal lobe function related to orienting of attention. On the other hand, the P3b is sensitive to the task relevance (or need for voluntary attention) of the stimulus, and is conceived as reflecting a post-identification process associated with event encoding or context updating (Debener et al., 2005; Dien et al., 2004; Friedman et al., 2001; Polich, 2003).

Considering that the effect of voluntary stimulus production occurred regardless of task relevance and that this effect was prominent at frontocentral sites in an earlier latency range of the P3 wave, the self-production of stimuli probably enhances the P3a component. However, it remains unclear whether the P3b component is unaffected or enhanced independently by voluntary stimulus production.

The present study was conducted to examine the effect of voluntary stimulus production on the P3 wave using a difficult three-tone oddball task, which is assumed to elicit the P3a and P3b components relatively independently (Comerchero and Polich, 1999). When the perceptual difference between standard and target stimuli is small and the difference between standard and task-irrelevant deviant stimuli is large, the P3 to high-deviant nontarget stimuli consists mainly of the P3a component, while the P3 to low-deviant target stimuli consists mainly of the P3b component (Katayama and Polich, 1998). Given that the P3a component is sensitive to voluntary stimulus production, the P3 to high-deviant nontarget stimuli is expected to increase in amplitude when the stimuli are triggered by participants' button presses. If this effect is specific to the response to contextually salient stimuli, the P3 to low-deviant target stimuli would be unaffected by the mode of stimulus presentation. Conversely, if voluntary production also modulates the response to task-related stimuli, the P3 to low-deviant target stimuli would also be increased. Besides testing these hypotheses, ERP differences before the onset of stimuli that were presented by participants or by a computer were examined. Movement-related potentials should be observed before the stimuli triggered by voluntary button presses.

2. Method

2.1. Participants

Sixteen student volunteers participated in the study (8 men and 8 women, 20–29 years old, mean 22.8 years). All were right-handed, assessed by a questionnaire (Oldfield, 1971). They had normal hearing assessed by standard audiometry. All participants signed informed consent.

2.2. Stimuli

Three types of pure tones were used: 1940 Hz (standard, $p = .750$), 2000 Hz (target, $p = .125$), and 500 Hz (deviant, $p = .125$). The combination of the tones replicated that used in the difficult condition of Comerchero and Polich (1999). All tones were 70 ms in duration (50 ms plateau, 10 ms rise/fall) and presented binaurally with two earphones (Sony MDR-EX70SL, Tokyo, Japan) at 60 dB SPL. Stimulus presentation was controlled with an audio-visual tachistoscope (Iwatsu-Isec IS702, Tokyo, Japan).

2.3. Procedure

Participants performed an auditory target detection task in two conditions. In the self condition, the stimuli were presented in response to participants' voluntary button presses. Each button press triggered one of the three stimuli within 10 ms after microswitch closure. Participants were instructed to press the trigger button with the index finger no quicker than once per 2 s. In the auto condition, the stimuli were presented automatically by the computer at the same interstimulus intervals as those recorded in the preceding self condition. In both conditions, participants were asked to press the response button to the target stimuli with the index finger on the other hand than the triggering finger as quickly and accurately as possible. Each condition consisted of 400 trials, which were divided into 5 blocks with 80 trials each (10 target, 10 deviant, and 60 standard stimuli). Participants performed five sets of the self and auto condition blocks alternately (10 blocks in total). The triggering and responding fingers were counterbalanced across participants. Before the experimental blocks, participants received short practice blocks for voluntary button presses and for stimulus discrimination. Participants performed all the tasks with their eyes open. At the end of the experiment, participants rated the difficulty of the self and auto conditions on a 9-point scale (1: easy – 9: difficult).

2.4. Electrophysiological recording

An electroencephalogram (EEG) was recorded from three midline sites (Fz, Cz, and Pz) referenced to the linked-earlobes using sintered Ag/AgCl electrodes. An electrooculogram (EOG) was recorded bipolarly from electrodes placed above and below the left eye. The bandpass filter was set at 0.016 Hz (time constant 10 s) to 60 Hz. The data were digitized at 250 Hz and stored on a hard disk for offline processing. The epoch between 200 ms before and 800 ms after stimulus onset was averaged separately for each participant, condition, stimulus, and site. In addition, the epoch between 1,000 ms before and 300 ms after stimulus onset was averaged collapsing across all stimulus types to examine the preparatory state before stimulus arrival. The epochs containing EEG or EOG over ±100 μV were removed automatically and those containing muscle artifacts were removed by visual inspection. The first 200-ms period of each waveform served as the baseline.

2.5. Data reduction

Trials that were too close to (< 2 s) or too remote from (> 10 s) the previous trials were excluded from the analysis (2.1 % of the total trials). Button presses occurring 200–1,200 ms after the target stimuli were regarded as correct responses. The mean reaction time was calculated for correct responses only. Button presses after the standard and deviant stimuli were counted as false alarms. Incorrect and false alarm trials were excluded from the ERP averaging.

To cancel out the movement-related potentials associated with a trigger button press and to eliminate possible differences in the baseline period between conditions, difference waveforms were calculated by subtracting the ERPs to standard stimuli from the ERPs to target and deviant stimuli. This procedure was applied to both the self and auto conditions, which allowed comparison of the deviance-related ERPs between the conditions (Nittono, 2004).

The peak latencies of the P3s were measured on the difference waveforms at the most dominant sites (Cz and Pz for the P3s to deviant and target stimuli, respectively). The time windows for peak detection were 248–420 ms and 300–540 ms for the P3s to deviant and target stimuli, respectively. The mean amplitude of five data points (±8 ms) around each peak was calculated at each electrode site. The mismatch negativity (MMN) and N2b, which had less clear peaks, were measured as the mean amplitudes of 100–148 ms and 152–200 ms for deviant stimuli and 100–196 ms and 200–296 ms for target stimuli, respectively. In addition, the second positivity that appeared after the P3 to deviant stimuli was measured as the mean amplitude of 448–548 ms.

2.6. Statistical analysis

Subjective and behavioral measures were compared between the self and auto conditions using two-tailed paired t tests. Amplitudes and latencies of ERP components were submitted to multivariate analyses of variance (MANOVAs) using Pillai's trace statistics. The statistical software package SAS ver. 8.02 (SAS Institute Inc., Cary, NC) was used with a significance level of .05. Multiple comparisons were made by the Bonferroni procedure (i.e., two-tailed paired t tests with a corrected comparison-wise significance level, $\alpha = .05/3 = .016$). ERP differences in the baseline period between the self and auto conditions were examined using point-by-point two-tailed paired t tests with a reduced significance level of .01.

3. Results

3.1. Subjective and behavioral measures

Mean trigger button press intervals, which were equal to the onset-to-onset stimulus intervals, ranged from 2,477 to 3,505 ms across participants (Mean 2,799 ms, *SD* 298). Table 1 shows the subjective and behavioral measures. The mean reaction time to target stimuli was longer in the self condition than in the auto condition, $t(15) = 2.18$, $p < .05$. The other measures did not differ significantly between the conditions.

3.2. ERP

Fig. 1 shows grand mean ERP waveforms. In both conditions, the N1 wave appeared after every type of stimulus with a peak latency of about 100 ms. Deviant and target stimuli elicited large positive waves (P3s) after that. ERP differences between the self and auto conditions started from the baseline period. Fig. 2 shows ERP waveforms from 1,000 ms before stimulus onset. Although the ERPs in the self and auto conditions were different, the epoch showing significant differences was rather short and started just 50 ms before stimulus onset. Even in the auto condition without triggering movement, a slow negative shift appeared particularly at Pz, starting from about 700 ms before stimulus onset.

Fig. 3 shows the difference waveforms calculated by subtracting the ERPs to standard stimuli from the ERPs to deviant and target stimuli, which are assumed to be free from the effects of movement-related potentials and possible ERP differences in the baseline. Deviant and target stimuli elicited large P3s. The P3 to deviant stimuli showed a larger amplitude in the self condition than in the auto condition, whereas the P3 to target stimuli did not. The P3 to deviant stimuli was followed by a second positivity, the amplitude of which was also larger in the self condition.

Fig. 4 illustrates the peak amplitudes of the P3s to deviant and target stimuli. A Stimulus × Condition × Site MANOVA on P3 amplitude showed a significant two-way interaction, $F(2, 14) = 8.04$, $p < .005$. Separate MANOVAs with factors of condition and site were then performed for deviant and target stimuli. For the P3 to deviant stimuli, there was a main effect of condition, $F(1, 15) = 32.97$, $p < .0001$, and a Condition × Site interaction, $F(2, 14) = 14.28$, $p < .0005$. Multiple comparisons showed that the effect of condition was significant at Cz and Pz, but not at Fz, and that the P3 to deviant stimuli had a central dominant scalp distribution (Fz < Cz and Fz < Pz in the self condition, Fz < Cz in the auto condition). P3 amplitude for target stimuli did not differ significantly between the conditions, Fs < 1 for the main and interaction effects. The effect of site was significant, $F(2, 14) = 25.74$, $p < .0001$. Multiple comparisons showed that the P3 to target stimuli had a parietal dominant distribution (Fz < Cz < Pz). Peak latencies of the P3s are shown in Table 1. A Condition × Stimulus MANOVA showed a significant effect of stimulus, $F(1, 15) = 131.62$, $p <.0001$, indicating that the P3 to deviant stimuli had a shorter peak latency than did the P3 to target stimuli. No significant main and interaction effects of condition were found, Fs(1, 15) = 1.16 and 0.34, respectively.

The second positivity was larger in the self than in the auto condition. A Condition × Site MANOVA showed a main effect of condition, $F(1,15) = 32.07$, $p < .0001$. The interaction was not significant, $F(2, 14) = 2.27$, $p = .14$. The effect of site was also significant, $F(2, 14)= 21.29$, $p < .0001$. Multiple comparisons showed that this positivity was dominant at the parietal site (Fz < Cz < Pz). MANOVAs on MMN and N2b amplitudes did not show any significant main or interaction effects of condition.

4. Discussion

High-deviant nontarget stimuli elicited a P3 with a shorter peak latency and more anterior scalp distribution than the P3 to low-deviant target stimuli. These results are consistent with the assumption that the P3s elicited by the deviant and target stimuli used in the present study consist mainly of the P3a and P3b components, respectively (Comerchero and Polich, 1999). The effect of voluntary stimulus production appeared clearly on the ERPs to deviant stimuli, that is, both the P3 and second positivity were enhanced in the self condition. The effect was not significant for the P3 to target stimuli. The mean reaction time to target stimuli was longer when participants triggered the stimuli, while P3 latencies to target and deviant stimuli did not differ between the conditions. As expected, movement-related potentials appeared before stimulus onset in the self condition, although reliable differences between the self and auto conditions were not observed until the last 50 ms.

4.1. P3 and second positivity

The increase of the P3 to high-deviant nontarget stimuli in the self condition supports the hypothesis derived from the previous studies (Nittono, 2004; Nittono and Ullsperger, 2000; Nittono et al., 2003), and indicates that the P3a component is enhanced by voluntary production of deviant stimuli. On the other hand, the finding of no significant difference in the P3 to low-deviant target stimuli suggests that the response to task-related stimuli is unaffected by self-production of stimuli. Although it seems plausible that voluntary attention is directed more efficiently to stimuli produced by voluntary action, this idea was not supported by the present findings.

Previously, the increase of P3 amplitude by voluntary stimulus production was explained in terms of the increase in stimulus timing certainty that makes neural activity more time-locked to the eliciting stimulus (McCarthy and Donchin, 1976; Nittono and Ullsperger, 2000). However, such a general explanation is insufficient to account for the result of this study. A more specific explanation is discussed later.

The P3 to deviant stimuli was followed by a second positivity with a parietal dominant scalp distribution, whose amplitude also was increased in the self condition. This second wave can be seen in the original study of Comerchero and Polich (1999), although the authors did not analyze this part of the ERP waveforms. A similar positivity is also found in other studies and considered as the P3b (Debener et al., 2005; Gaeta et al., 2003). The parietal dominant distribution of this potential resembles that of the P3 to target stimuli, which consists mainly of the P3b component. Therefore, it is likely that voluntary stimulus production can enhance the P3b component when the stimulus is salient enough to elicit the P3a, while the P3b is not affected independently by voluntary stimulus production. Moreover, close inspection of the P3 to deviant stimuli reveals that the amplitude increase occurred at centroparietal sites. This pattern of result suggests that the P3b component might have been enhanced even from an earlier latency range overlapping with the initial P3 wave.

4.2. Reaction time and P3 latency

The mean reaction time was longer when the stimuli were triggered by participants than when presented automatically, whereas the peak latency of the P3 did not differ between the conditions. This pattern of results was obtained in previous studies (Nittono, 2004; Nittono and Ullsperger, 2000), and suggests that the reaction time difference occurs in a later stage of processing, probably due to the motor conflict between the right and left fingers used to trigger the stimulus and respond to the target. This difficulty was reported by several participants and was reflected in a higher (though not significantly) subjective rating score in the self condition than in the auto condition. The prolonged reaction time is not the main cause of the P3 enhancement, because the latter effect is also observed in counting tasks that do not require motor responses (McCarthy and Donchin, 1976; Nittono et al., 2003).

4.3. Prestimulus ERPs

It is known that a voluntary movement is preceded by several negative potentials (Shibasaki et al., 1980). In the present study, movement-related potentials were observed at frontocentral sites. Unexpectedly, a negative slope appeared similarly in both the self and auto conditions, starting from about 700 ms before stimulus onset. This negative potential is dominant at the parietal site (Pz), and is thought to be the stimulus preceding negativity (SPN), which reflects anticipatory attention for the upcoming stimulus (Brunia and van Boxtel, 2001). The occurrence of such a clear SPN is partly due to the experimental settings specific to the present study, that is, a difficult discrimination task with relatively long interstimulus intervals (Mean 2,799 ms). Nevertheless, it is noteworthy that substantial activity can occur before stimulus onset even during the usual oddball task in which the stimuli are presented automatically.

4.4. Possible mechanism and implications

Considering that the self and auto conditions were exactly the same except for the mode of stimulus presentation, it is unlikely that there are two different routes of stimulus processing. At least where the P3 is concerned, voluntary stimulus production probably modulates the existing ERP components rather than elicits a new, qualitatively different component. Given that the P3a is a part of an orienting response, there should be a certain mental representation or neuronal model of the stimulus context, in which case deviance elicits an orienting response. In a recent review, Polich

(2003) suggests that the P3a occurs "when incoming stimuli replace the contents of working memory" (p. 91). Essentially, this representation is in the realm of perception and is formed regardless of action. The findings of the previous and present studies suggest that this perceptual representation is affected by the voluntary action of producing the stimuli, and thus require a theoretical framework explaining the link between perception and action.

A good candidate for this framework is the *common coding* theory, which holds that action and perception share a common representation, which may prime or interfere with each other (Prinz, 1997; for an integrative review see Hommel et al., 2001). In principle, any voluntary action is preceded by the idea of its end or some anticipatory image of its sensorial consequences (James, 1890). According to this ideomotor principle, the perceptual representation of a forthcoming stimulus is activated before its arrival when a participant intends to produce it by voluntary action. The frequent experience of a perceptual event after a certain action strengthens the bidirectional link between action and effect through associative learning mechanisms (Elsner and Hommel, 2001, 2004). Although it is controversial whether this learning process takes place automatically or selectively (Ziessler et al., 2004), it is plausible that action (or action planning) activates the perceptual representation of a forthcoming event that depends largely on frequent stimuli. This anticipatory activation would make a deviant stimulus more salient in the context and elicit a larger orienting response (reflected in a larger P3a) and subsequent updating of the representation (reflected in a larger P3b).

Although the present study does not provide direct evidence for this anticipatory activation process, future studies could visualize it using high-density EEG recording and sophisticated component separation techniques (e.g., Makeig et al., 2004). In a study using positron emission tomography, brain areas including the medial posterior cingulate cortex showed a higher activation when participants generated single tones by voluntary action than when they heard the same tones presented in a predictable regular interval (Blakemore et al., 1998). The higher temporal resolution of the ERP may be useful to specify the timing of this activation, which is hard to achieve using hemodynamic functional brain imaging. Also, EEG source separation techniques appear to be helpful to dissociate early cognitive ERP components from movement-related components, which could not be done effectively with the traditional subtraction method used in the present study.

There is still a possibility that the present results are not specifically related to voluntary stimulus production. The frontocentral P3a is shown to be elicited when the oddball task requires a lot of attentional resources and a physically salient distracting stimulus disrupts the enhanced focal attention (Katayama & Polich, 1998; Polich, 2003). Voluntary actions to produce stimuli may be merely one of the many factors that serve to increase the allocation of attentional resources to the oddball task. Even if this generic account were correct, the validity of the main finding of this study, that voluntary action affects stimulus processing, would be unaffected.

4.5. Conclusion

The present study provides convincing evidence that the P3 (P3a) to deviant stimuli is enhanced when participants produce the stimuli by voluntary action. The P3b component is not affected independently by voluntary stimulus production, but can be enhanced when the stimulus is salient enough to elicit the P3a.

In most of the current studies on the top-down attentional set, motor components are typically excluded to make the analysis simpler (e.g., Corbetta and Shulman, 2002). However, cognition in everyday life is often coupled with voluntary action. Recording brain activity during interactive tasks in which participants get information by voluntary action is a useful step to reveal new aspects of human cognition, which should be eventually integrated into current theories of attention.

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Table 1. Difficulty ratings, error rates, mean reaction times, and P3 latencies in the self and auto conditions.

	Condition			
	Self		Auto	
Difficulty (1: easy – 9: difficult)	4.7	(1.9)	4.1	(2.1)
Error rate (%)				
Miss to target	9.0	(9.4)	12.0	(11.9)
False alarm to standard	1.4	(2.5)	2.1	(3.7)
False alarm to deviant	0.1	(0.6)	0.8	(1.5)
Mean reaction time (ms)	624	(115)	588	(90) *
P3 latency (ms)				
Deviant	303	(33)	313	(34)
Target	447	(46)	450	(48)

Note: Standard deviations are shown in parentheses.

*Significant difference between the self and auto conditions, $p < .05$.

Figure Captions

Fig. 1. Grand mean ERP waveforms in the self and auto conditions ($N = 16$). Vertical lines indicate the onset of stimuli. In the self condition, the stimuli were presented within 10 ms after the microswitch closure of the trigger button.

Fig. 2. ERP waveforms before stimulus onset in the self and auto conditions. Vertical lines indicate stimulus onset. Thick horizontal bars indicate the time points showing a significant difference between the conditions, $p < .01$.

Fig. 3. Difference waveforms calculated by subtracting the ERPs to standard stimuli from the ERPs to deviant and target stimuli.

Fig. 4. P3 amplitudes for deviant and target stimuli and the mean amplitudes of the second positivity (448-548 ms) for deviant stimuli. Vertical bars indicate standard errors. Asterisks show significant differences between the conditions, $p < .05$.

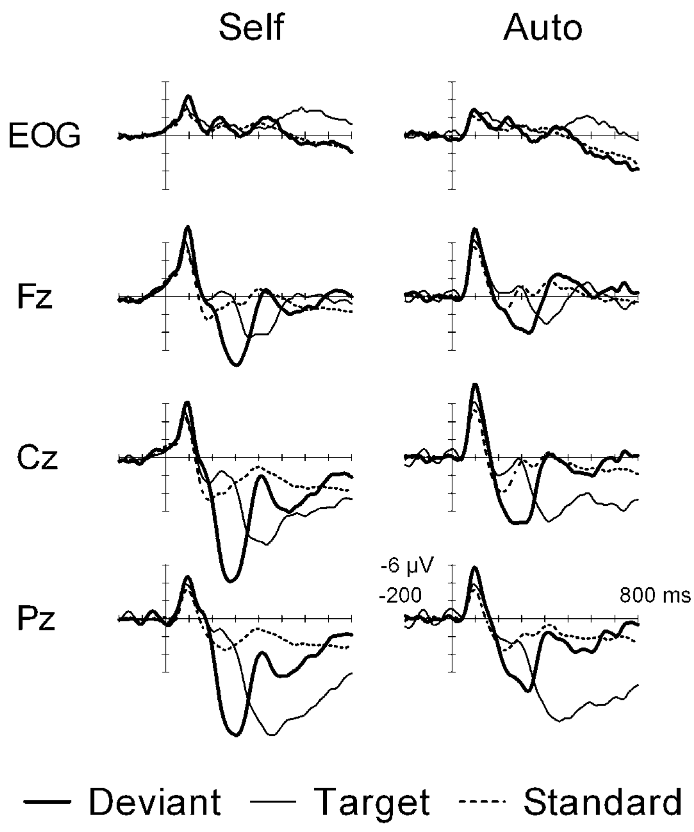


Fig. 1

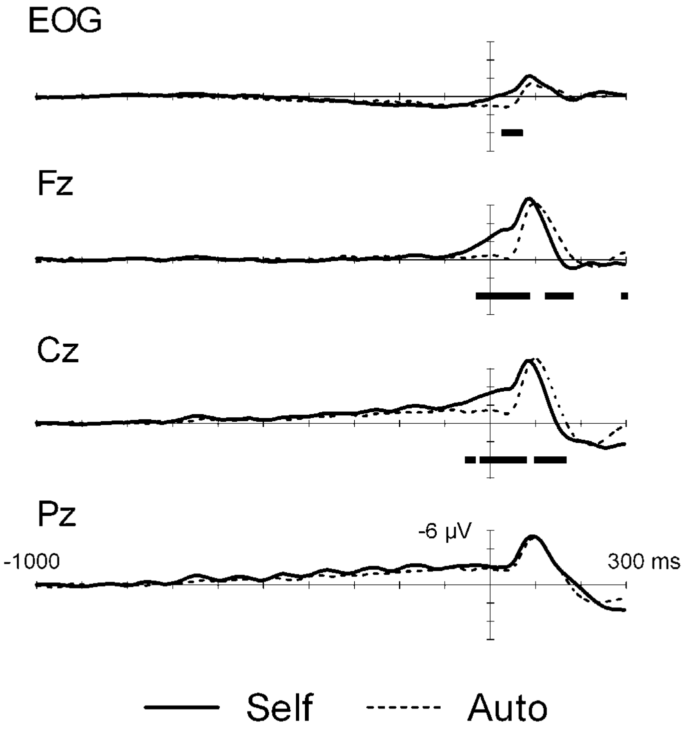
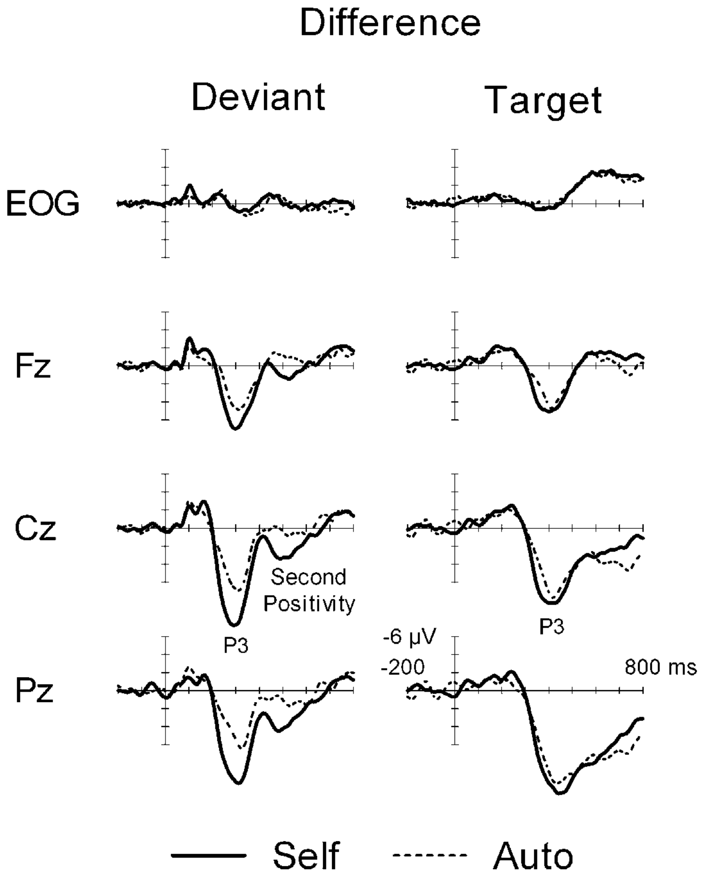


Fig. 2


Difference
Deviant
Target
EOG
Fz
Cz
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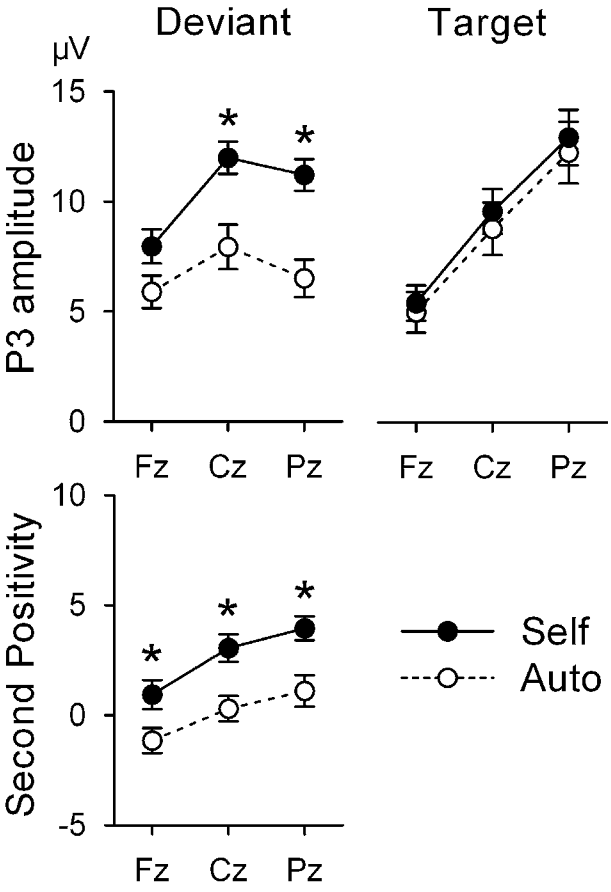
Positivity
P3
P3
-6 μV
-200
800 ms
Self
Auto

Fig. 3


Deviant
Target
μV
P3 amplitude
15
10
5
0
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Fz
Cz
Pz
Fz
Cz
Pz
Second Positivity
10
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-5
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Fz
Cz
Pz
Self
Auto

Fig. 4