Effects of Target Stimulus on Sympathetic Skin Response in Counting and Reaction Tasks

Masahiro SHIMODA[1], Kuniyasu IMANAKA[2], Yoshiaki NISHIHIRA[3], Ichiro KITA[2], Arihiro HATTA[3], Masaki FUMOTO[4], Takeshi KANEDA[4], Sachiyo AKIYAMA[4] and Shinichiro TOKITO[4]

[1] *Health and Amenity Science, Faculty of Agriculture, Tokyo University of Agriculture and Technology, 3-5-8 Saiwai-cho, Fuchu 183-8509, Tokyo, JAPAN*
[2] *Department of Kinesiology, Faculty of Science, Tokyo Metropolitan University, 1-1 Minami-Ohsawa, Hachioji 192-0364, Tokyo, JAPAN*
[3] *Institute of Health and Sport Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba 305-8574, Ibaraki, JAPAN*
[4] *Doctoral Program in Health and Sport Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba 305-8574, Ibaraki, JAPAN*

Abstract

SHIMODA, M., IMANAKA, K., NISHIHIRA, Y., KITA, I., HATTA, A., FUMOTO, M., KANEDA, T., AKIYAMA, S. and TOKITO, S., Effects of Target Stimulus on Sympathetic Skin Response in Counting and Reaction Tasks. Adv. Exerc. Sports Physiol., Vol.7, No.3 pp.93-101, 2001. To examine the effects of motor responses to target stimuli on elicitation of sympathetic skin response (SSR), we assessed both the N140 and P300 components of event-related brain potentials (ERPs) and SSR of ten healthy volunteers using an oddball paradigm in two types of conditions. In one condition, subjects were required to count the target stimuli (count condition), while in the other condition, the subjects were asked to perform a quick voluntary movement in response to the target stimuli (reaction condition). Amplitudes of both N140 and SSR were larger in the reaction condition than in the count condition. The amplitude of P300 did not significantly change in either condition. The latency of P300 decreased in the reaction condition rather than in the count condition. Thus, it is likely that the target stimuli presented in the count condition may be processed with the same amount of attentional resources of subjects as in the reaction condition, but the requirement of a quick motor response may resulted in different meanings of the target stimuli for the reaction and count conditions. In conclusion, it is considered that the requirement of quick motor responses enhances both the arousal state of subjects and the stimulus meaning which indicates that the subjects should perform a voluntary movements itself, and that these enhancements may then activate the sympathetic nerve responses (e.g., SSR).

Keywords: sympathetic skin response (SSR), event-related brain potentials (ERPs), stimulus meaning, arousal, voluntary movements

Introduction

The sympathetic skin response (SSR) is thought to be a useful index of sudomotor sympathetic function. The SSR is well observed when an unpredictable signal (stimulus), such as a stimulus presented at an interval longer than 30 s, is presented to subjects. In such a condition, it is often observed that amplitudes of SSR decrease as the number of stimulus presentations increase (25). This phenomenon is called the 'habituation' of SSR (2, 3). It is suggested that the habituation of SSR may appear because the subjects cannot continue to direct their attention to all of the stimuli presented in the experiment. It is therefore considered that the control of SSR (i.e., sympathetic nerve activity) may be affected by the central nervous systems (e.g., 22, 25). Furthermore, if it could avoid the habituation phenomena in recording SSRs, the use of SSR would become more valuable in evaluating the sympathetic function (e.g., 2, 4).

To avoid such habituation phenomena in recording SSRs, Aramaki et al. (2) has suggested that a method of averaging using target and standard stimuli may be considered. In this method, both target and standard stimuli that differ in the probability of their presentation are used. The target stimuli, which subjects are required to detect, are presented at a low probability, such as 20% of all stimuli presented in an experimental session, and are thus called 'rare' target stimuli. The standard stimuli, which subjects are asked to ignore, are presented at a high probability (e.g., 80%). Under these stimulus conditions, the SSR well appears with the rare target stimuli rather than the standard stimuli. Such a stimulus-presentation method is generally similar to the stimulation sequence of the 'oddball' paradigm, which is typically used to record the P300 components of event-related brain potentials (ERPs). In fact, Deguchi et al. (9) and Knight (19) have recently shown that both the SSR and P300 are concurrently evoked by rare target stimuli in the oddball paradigm.

In general, the use of rare target stimuli in the oddball paradigm require subjects to either consciously detect each rare target stimulus among other nontarget stimuli (this is called the "counting task") or respond to the rare target stimuli by producing movements (the "reaction time task" or "RT task"). Although both the counting and RT tasks are well known to contribute to evoking the P3b, a type of

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Address for Correspondence: Masahiro Shimoda, Ph.D., Health and Amenity Science, Faculty of Agriculture, Tokyo University of Agriculture and Technology, 3-5-8 Saiwai-cho, Fuchu 183-8509, Tokyo, JAPAN.
Tel: +81 42 367 5642
Fax: +81 42 367 5648
E-mail: shimoda@cc.tuat.ac.jp

P300 (7, 28), it is still unclear whether the counting (i.e., target detection) is much more effective in evoking SSRs than the RT task (i.e., movement production), or vice versa.

For evoking P3b, the counting task has often been used to require subjects to allocate their attentional resources to the given stimuli alone. In the counting task, subjects are asked to count in mind the number of target stimuli presented among a large number of nontarget (standard) stimuli and the subjects thus attempt to be attentive to detect each target stimulus. The rare target stimulus is therefore thought to enhance subjects' attention. Such an effect of the rare target stimuli on the subjects' attention is termed the 'target effect' (13, 18, 29).

Although the target effect has typically been observed in counting tasks, the target effect has also been suggested by Tueting and Sutton (34) to occur in RT tasks as well. Tueting and Sutton (34) showed that a typical P3b appeared when subjects were required to make a motor response to, rather than counting, each target stimulus. However, it has been suggested that there is a slight difference in the amplitude of P3b between the counting and RT tasks (5, 17). Both Barrett et al. (5) and Johnson (17) showed that the P3b amplitudes for rare target stimuli appeared larger under RT tasks than under counting tasks. Such a difference in the amplitude of P3b indicates that the meaning (or function) of the target stimuli under counting tasks may differ from that under RT tasks. The requirement of motor responses involved in RT tasks may provide the target stimuli with some specific meaning.

Roth (30) suggested that the 'signal value' and the direction of attention were directly linked to the nature of the task in which the subjects were asked to perform a motor response, and that such task-relevant factors (i.e., signal value and the direction of attention) were responsible for the P3b appearance. Johnson (17) also suggested that the 'stimulus meaning' is one of the factors determining the P300 amplitude[‡]. The requirement of motor response in RT task may probably result in providing the stimulus meaning specific to movement production in addition to the stimulus meaning specific to target detection, as seen in counting tasks. The stimulus meaning specific to movement production may well differ from the stimulus meaning under counting tasks.

Regarding the SSR in the context of motor response, it has been shown that the electrodermal activities (EDAs) are also enhanced when subjects are required to make a motor response. Bernstein and Taylor (6) showed that skin conductance responses (SCRs, a type of EDAs) were larger in amplitude when subjects were asked to respond to target stimuli with a pedal-pressing response than for those without that motor response. Siddle et al. (32) also reported that subjects who were asked to perform a quick RT response showed larger SCRs than those without any motor response. These findings suggest that the electrodermal responses are enlarged when subjects make a motor response, and that it is the motor-related nature of the given stimulus that may affect the electrodermal responses. In addition, Osada et al. (26) have recently shown that SSR appears with both the bereitschaftspotential (BP, 20) and event-related desynchronization (ERD) of the EEG (27) during a self-paced voluntary movement. Both the BP and the ERD are thought of as a manifestation of the neural preparatory processes for the production of voluntary movements. The findings of Osada et al. (26) therefore imply that the movement-related processes of information processing may affect the SSR as well as the SCR.

However, it is still far from clear that how the movement-related processes, such as conscious detection of target stimuli and the production of motor response, influence the elicitation of SSR. In the present study, the significance of both conscious target-detection and motor response on elicitation of SSR was examined to elucidate the contribution of movement-related brain functions to the sympathetic nerve activity. To examine this issue on SSR, an oddball paradigm was used under two conditions with multiple measurements of SSR and several ERP components. In one condition (count condition), subjects were asked to count the number of target stimuli presented in the oddball paradigm experiment, while in the other condition (reaction condition), the subjects were asked to respond by extending their elbow to each target stimulus as quickly as possible. In both conditions the target stimuli should invoke target-detection processes in the brain, while in the reaction condition alone the target stimuli may invoke additional motor processes that relate to voluntary movements. These predictions were examined by a comparison of P300 components for target stimuli between the count and reaction conditions.

In addition to the P300 components, N140 component of ERPs was also measured in this experiment. The N140 component is sensitive to whether subjects attend to given stimulus (10, 15, 16). Both P300 and SSR are believed to be mediated, in part, by subjects' attention. To assess the attentional allocation of the subjects for the stimuli in both the count and reaction conditions, the N140 components were measured.

Methods

Subjects

Ten neurologically normal volunteers (eight males

[‡] The term 'signal value' (30) is considered to be identical to the term 'stimulus value' originated by Johnson (17), who proposed the stimulus value as one of the variables indicating/measuring the degree of stimulus meaning. Therefore, in the present study, we deal with both the terms "signal value" and "stimulus value" as indicating the "stimulus meaning".

and two females), aged from 20 to 29 years, participated in this experiment. Informed consent was obtained from each participant.

Recordings of EEG, EMG, and SSR

Nine Ag/AgCl disk electrodes for recording EEG were placed on F3, Fz, F4, C3, Cz, C4, P3, Pz and P4. The EEG signal was amplified through a bandpass filter with a range of 0.53 to 120 Hz. To monitor possible artifacts due to eye movements, electro-oculogram (EOG) was recorded using electrodes placed above and below the left eye. EMG was recorded using two pairs of surface electrodes placed on both the triceps and the biceps muscles of the right arm and amplified through a bandpass filter with a range of 5.3 to 1500 Hz. SSR was recorded using Ag/AgCl disk electrodes placed on both palmar and dorsal sites of the left hand and was amplified through a bandpass filter with a range of 0.53 to 1500 Hz. Electrical square stimuli of 0.2 msec in duration were generated using two electrical stimulators (3F46, NEC San-ei Co. Ltd., Japan). Each stimulator delivered electrical stimuli to either the index or little finger of the right hand using ring electrodes attached at the middle of the first (cathode) and second phalanx (anode) of each finger. The intensity of these stimuli ranged from two to three times the subjective sensory threshold of each finger, that is, the intensity quite strong but certainly not painful. All analog signals including the electrical signals of each stimulus were recorded both on recording paper fed from an EEG recorder (EE1121A, NEC San-ei Co. Ltd., Japan) and on the magnetic tape of a data recorder (PC216Ax, Sony Precision Technology Inc., Japan).

Procedures

Subjects were comfortably seated in an armchair. A pile of rectangular stainless-steel plates was fixed on the right armrest. Between the two plates was a short piece of wood at one end. A strain gauge was attached on the upper plate to detect deformation of the plate. The subjects put their right forearm on the upper plate and were instructed to keep their eyes open and maintain a stable arousal level of consciousness during experimental trials. After a 10-minute resting period, an oddball-paradigm experiment was performed under two conditions (count and reaction conditions). In both conditions, more than 100 electrical stimuli were delivered to either the index (target, 20%) or the little (standard, 80%) finger at a fixed interstimulus interval (3 sec). The interstimulus interval was used to record SSR waves clearly without any superimposition of the previous SSR wave evoked by the preceding target stimulus. In the count condition the subjects were asked to count the number of target stimuli while in the reaction condition they were asked to respond to the target stimuli by extending the right elbow joint to press down on the upper plate as quickly as possible. The subjects were also instructed to ignore any of the standard stimuli in either condition. After the completion of the count condition, experimenter required the subjects to answer the number of target stimuli. These two conditions were presented in an order counterbalanced between subjects.

Analyses of N140, P300, and SSR

After completion of the experiment, EEG and SSR analog signals stored on magnetic tape were converted into digital data at a sampling rate of 200 Hz through an A/D converter installed on a personal computer (PC9821 Xa7, NEC Co. Ltd., Japan). Digital data were analyzed with a signal-processing software (EPLYZER, Kissei Comtec Co. Ltd., Japan). EEG data converted for 800 msec (ranging from 200 msec before the stimulus onset to 600 msec after the stimulus onset) were averaged over 16 samples for target stimuli and over 75 samples for standard stimuli. N140 and P300 components of ERPs were defined as peak amplitudes that appeared in two different post-stimulus windows ranging from 120 to 160 and 245 to 450msec, respectively. The amplitudes of N140 and P300 were measured from a 200-msec prestimulus baseline. The latencies of N140 and P300 were measured as the time elapsing from the stimulus onset to the peak amplitude. SSR data were converted for 4500 msec (ranging from 0 msec to 4500 msec after the stimulus onset) because one waveform of SSR is often terminated about 4000 msec after the stimulus onset. Therefore, the averaging of SSR data was performed two times: over 16 samples with target stimuli and 75 samples with standard stimuli. The amplitude of SSR was measured as a peak-to-peak difference of the averaged waves. In order to eliminate possible artifacts on the averaged waveforms of both ERPs and SSR, trials with either excessive muscle activity or eye blinks (detecting from EMG and EOG) were excluded from these measurements.

Statistics

Three-way ANOVAs were performed on each of the amplitudes and latencies of N140 for the following repeated-measures factors: condition (C; reaction and count), stimulus (S; target and standard) and electrode (E; F3, Fz, F4, C3, Cz, C4, P3, Pz and P4). Two-way ANOVAs were also performed on each of the amplitude and latency of P300 for both condition (C) and electrode (E) factors because the present study dealt with the P300 components for the target stimuli. When the main effect of electrode factor was significant, contrast tests were then performed for the electrode effects. To decrease the experiment-wise error rate due to the repeated-measures design involving multiple dependent variables, a Greenhouse-Geisser adjustment for the degree of freedom was performed. The Student's paired *t*-test was used to compare the effects of the two conditions on the amplitudes of SSR for the target stimulus. A level of $p < 0.05$ was accepted as indicating statistical significance.

Results

In the count condition, the subjects accurately answered the number of target stimuli. Figure 1 and Figure 2 show typical recordings of both ERPs and SSR under each condition in one subject.

N140 components

For the amplitudes of N140 (Table 1), the main effect for conditions was significant (F=10.858, $p<0.01$) with the N140 amplitudes in the reaction condition being significantly larger than those in the count condition. The main effect for electrodes was also significant (F=4.802, $p<0.05$). Contrast tests were then calculated among the electrode sites. The results revealed that the N140 amplitudes at all frontal and central electrode sites except C3 were significantly larger than those at parietal sites ($p<0.05$). There were no lateral differences for the N140 amplitudes.

For the latencies of N140 (Table 2), the main effect for electrodes was significant (F=10.649, $p<0.001$). Contrast tests were then calculated among electrode sites. The results were as follows: i) at midline sites, the N140 latencies at Cz was shorter than those at Pz and Fz (Cz vs. Pz, $p<0.05$; Cz vs. Fz, $p<0.001$; Pz vs. Fz, $p<0.05$); ii) at both left and right sites, the N140 latencies at central and parietal sites were shorter than those at frontal sites (left, C3 vs. F3, $p<0.01$; P3 vs. F3, $p<0.05$; right, C4 vs. F4, $p<0.05$; P4 vs. F4, $p<0.05$); and iii) the N140 latencies at C3 were shorter than those at C4 ($p<0.01$).

P300 components

P300 components of ERPs clearly appeared for target stimuli (Figure 1). For the P300 amplitudes (Figure 3, Table 3), the main effect was significant for electrodes (F=28.341, $p<0.001$) but not for conditions. Contrast tests were then calculated for the electrode effects. The results showed that the mean P300 amplitudes were significantly greater for all the parietal sites compared with the frontal

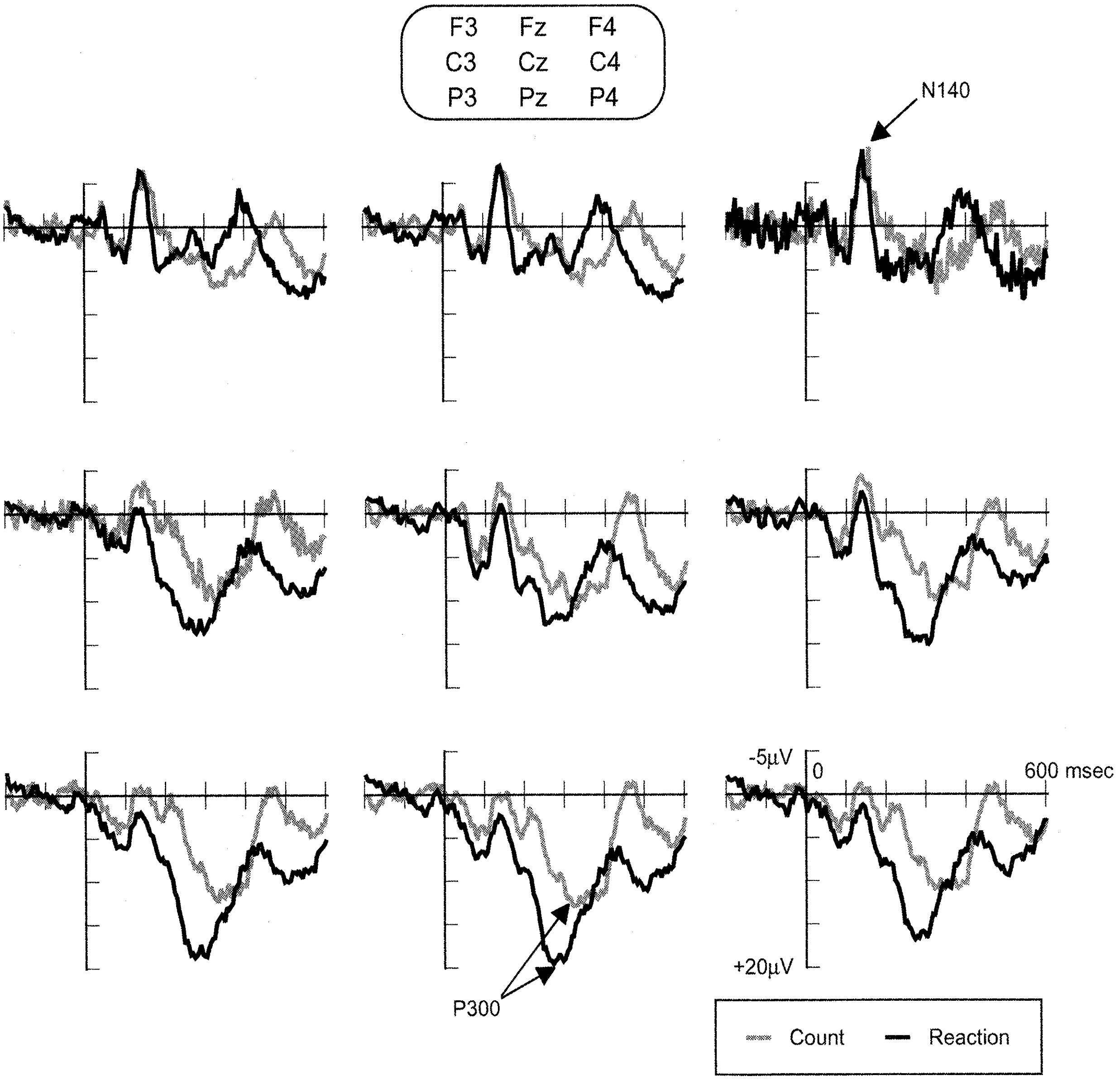

Figure 1 Typical recordings of ERPs for the target stimuli in Count and Reaction conditions.

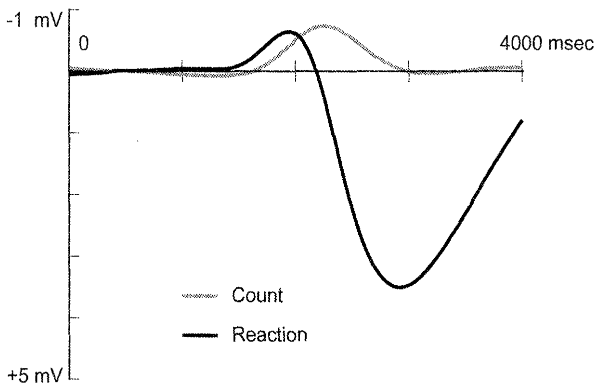

Figure 2 Typical recordings of SSRs for the target stimuli in Count and Reaction conditions.

Table 1 The amplitudes of N140 (μV) for the standard and target stimuli in Count and Reaction conditions.
Note gives a summary of the ANOVAs for both significant main effect for both condition (C) and electrode (E) on the N140 amplitudes.

Electrode	Standard		Target	
sites	Mean	SD	Mean	SD
Count				
F3	-2.725	2.538	-3.499	3.547
Fz	-3.496	2.712	-3.741	3.518
F4	-4.058	2.638	-4.006	3.717
C3	-2.243	3.011	-2.769	4.904
Cz	-2.714	4.157	-2.442	6.547
C4	-3.746	2.092	-3.734	4.032
P3	-0.860	2.947	-1.372	4.993
Pz	-0.507	2.511	-0.945	4.812
P4	-1.680	1.797	-1.487	4.114
Reaction				
F3	-4.340	4.815	-5.479	4.096
Fz	-5.393	4.556	-5.793	3.686
F4	-5.887	3.836	-6.690	4.007
C3	-3.845	4.341	-4.745	4.513
Cz	-5.335	5.813	-6.540	6.209
C4	-5.383	3.643	-6.788	3.987
P3	-2.466	3.820	-3.193	4.782
Pz	-2.409	3.686	-3.604	4.508
P4	-3.185	3.298	-4.039	3.781

Note: $F = 10.858, p < 0.01$, for Condition
$F = 4.802, p < 0.05$, for Electrode

sites (except Pz vs. Cz, $p=0.12$) (for the midline, Fz vs. Cz, $p<0.001$, and Fz vs. Pz, $p<0.001$; for the left, F3 vs. C3, $p<0.01$, C3 vs. P3, $p<0.05$, and C3 vs. P3, $p<0.001$; for the right, F4 vs. C4, $p<0.01$, F4 vs. P4, $p<0.001$, and C4 vs. P4, $p<0.05$).

For the P300 latencies (Figure 3, Table 4), the main effect for conditions was significant ($F=12.968$, $p<0.01$) with the P300 latencies in the reaction condition being shorter than those in the count condition.

Table 2: The latencies of N140 (msec) for the standard and target stimuli in Count and Reaction conditions.
Note gives a summary of the ANOVAs for a significant main effect for electrode (E) on the N140 latencies.

Electrode	Standard		Target	
sites	Mean	SD	Mean	SD
Count				
F3	136.5	14.729	136.5	13.550
Fz	140.0	13.540	138.5	14.152
F4	139.5	13.834	139.0	13.904
C3	128.5	12.483	129.0	17.127
Cz	131.5	16.841	127.5	13.794
C4	135.5	13.834	133.0	16.021
P3	131.5	17.646	130.5	18.174
Pz	134.0	16.799	134.0	18.679
P4	136.5	14.539	131.5	16.338
Reaction				
F3	130.5	12.791	139.5	13.427
Fz	139.5	11.891	139.5	13.834
F4	138.5	14.916	137.0	12.953
C3	124.0	14.298	134.0	14.870
Cz	129.0	14.298	133.0	11.106
C4	134.0	14.103	135.5	16.236
P3	127.0	14.944	135.0	15.092
Pz	132.0	17.826	138.5	13.754
P4	131.0	19.120	137.0	14.944

Note: $F = 10.649, p < 0.001$, for Electrode

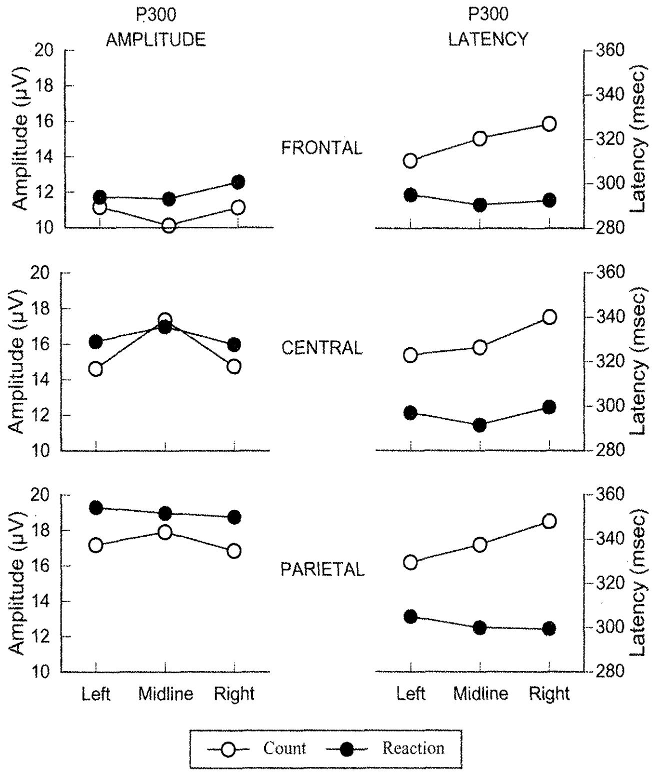

Figure 3 Mean amplitudes and latencies of P300 for target stimuli in Count and Reaction conditions as a function of coronal electrode site for the frontal, central, and parietal electrode positions.

Table 3 The amplitudes of P300 (μV) for the target stimulus in Count and Reaction conditions.
Note gives a summary of the ANOVAs for a significant main effect for electrode (E) on the P300 amplitudes.

Electrode sites	Count Mean	Count SD	Reaction Mean	Reaction SD
F3	11.166	4.049	11.725	4.260
Fz	10.129	3.912	11.618	3.682
F4	11.127	4.187	12.561	3.650
C3	14.619	3.957	16.151	2.414
Cz	17.353	5.254	16.978	3.976
C4	14.751	3.446	15.981	3.406
P3	17.177	5.266	19.290	2.989
Pz	17.904	5.274	18.963	3.376
P4	16.846	5.711	18.752	4.293

Note: $F = 28.342, p < 0.001$, for Electrode

Table 4 The latencies of P300 (msec) for the target stimulus in Count and Reaction conditions.
Note gives a summary of the ANOVAs for a significant main effect for condition (C) on the P300 latencies.

Electrode sites	Count Mean	Count SD	Reaction Mean	Reaction SD
F3	310.5	39.823	295.0	45.583
Fz	320.5	48.788	290.5	48.503
F4	327.0	37.133	292.5	44.985
C3	323.0	32.421	297.0	43.856
Cz	326.5	31.715	291.5	52.707
C4	340.0	26.667	299.5	41.463
P3	329.5	28.132	305.0	47.022
Pz	337.5	28.988	300.0	47.668
P4	348.0	18.738	299.5	47.752

Note: $F = 12.968, p < 0.01$, for Condition

Table 5 The amplitudes of SSR (mV) to the target stimuli in Count and Reaction conditions.
Asterisk shows a significant difference of SSR amplitudes between the two conditions.

	Count Mean	Count SD	Reaction Mean	Reaction SD
SSR*	0.417	0.126	2.393	0.757

*: $p < 0.001$

SSR

In both conditions, target stimuli evoked clear SSR waveforms (Figure 2), but standard stimuli did not. The Student's paired *t*-test revealed that the amplitudes of SSR in the reaction condition were significantly larger than those in the count condition ($p < 0.001$, Table 5).

Discussion

The purpose of this experiment was to examine the effects of motor response to target stimuli on elicitation of SSR. In both the count and reaction conditions, large P300 components were evoked by target stimuli. Both the scalp distribution and the amplitude of the P300 component in the reaction condition appeared similar to those in the count condition, whereas the latency of the P300 component in the reaction condition differed from that in the count condition. These P300 components could be identified as P3b because they were evoked by task-relevant stimuli and had maximum peaks at parietal sites (28). On the other hand, SSR evoked by target stimuli in the reaction condition was larger than that in the count condition. First, the results of N140 and P300 will be discussed in terms of the stimulus nature of the target stimuli which should be involved in these two conditions. Following this, the effects of motor response on elicitation of SSR will be discussed.

The amplitudes of N140 components, which are attention-sensitive, were larger in the reaction condition than in the count condition, and larger at the frontal and central electrode sites than at the parietal sites. Either the frontal (1, 11) or the central area (the secondary somatosensory cortex, 33) is suggested to be the source area of N140 and to contribute to generating human attention and intention. The results on N140 therefore imply that the attentional level or arousal state of the subjects was higher in the reaction condition than in the count condition (10, 15, 16).

The latencies of P3b appeared shorter in the reaction condition than in the count condition. This indicates that the time spent in both evaluating the meaning of stimulus (21) and updating the cognitive context, such as updating the memory of a given stimulus after evaluating incoming information of the stimulus (12), was shortened in reaction condition. Some researchers (5, 17) showed that P3b clearly appeared when target stimuli were presented in both count and reaction conditions. Barrett et al. (5) also showed that P300 latencies for target stimuli in the reaction condition were shorter than those in the count condition. Barrett et al. then suggested that subjects tended to respond 'faster' when the subjects were required to make a motor response to the target stimuli than when they were asked to count them. In the present experiment, subjects were asked to detect target stimuli in both conditions, whereas only in reaction condition alone they were also asked to produce a voluntary movement as quickly as possible. It is therefore suggested that the requirement of quick motor response (such as that required of the subjects of the present experiment) may cause acceleration in information processing of the stimuli, thus resulting in the short latencies of P3b components.

In contrast, it has also been suggested that the latency of P300 is not affected by the nature of information processing specific to motor response (21) and that P300 is sensitive to stimulus evaluation but not to response selection processes (14, 24). Although it is therefore necessary to further examine both the significance of target stimuli (i.e., 'stimulus meaning' 17) and the effects of motor production on P300, both may be inherent in the target stimuli, given the speed-maximizing instruction (i.e., requiring the subjects to respond as quickly as possible) in this experiment.

For the amplitude of P3b, Barrett et al. (5) showed that P300 amplitudes appeared larger for a button-press response than for a count response. Johnson (17) showed differences in P300 amplitude that were recorded under count, reaction, and feedback conditions†: the P300 amplitude was the least for the count condition, medium for the reaction condition, and largest for the feedback condition. Johnson suggested that the degree of 'processing-demands' (i.e., processing or attentional resources) associated with these tasks would follow the same order as shown by P300 amplitude (i.e., counting < reaction < feedback), and that the P300 amplitude increased as the task complexity increased. In contrast to the results of Barrett et al. (5) and Johnson (17), the amplitudes of P3b for target stimuli obtained in the present experiment did not differ between count and reaction conditions, suggesting that the requirement of motor response as the meaning of target stimuli may not have affected P3b amplitudes.

A possible explanation for the absence of differences in P3b amplitude between the count and reaction conditions is that the interstimulus interval (3 sec) of the oddball paradigm used in this experiment was longer than that commonly used in a number of studies (e.g., 1.4 sec in Barrett et al., 1987 and 1.705 sec in Johnson, 1986). An interstimulus interval was used in this experiment so that SSR waves could be clearly recorded without any superimposition of the previous SSR evoked by the preceding target stimulus. During this long interval, the subjects were necessarily forced to maintain in memory the number of target stimuli. Thus, the subjects should have maintained their memory of the sequential number of a given target stimulus for, at least, six seconds. On the other hand, in the reaction condition, such memory-related effects could never arise because the subjects responded to each target stimulus once at a time. The requirement of memorization in the count condition may therefore have caused the task to be more complex than in the reaction condition. Such a memory load in the count condition can be characterized as an additional task complexity, thus resulting in an equivalent P3b amplitude to that in reaction condition. In fact, after the completion of the experiment, the subjects introspectively reported that it was more difficult to remember the number of target stimuli (count condition) than to respond simply to them (reaction condition).

In addition, the prolonged P3b latency in the count condition seems to indicate that subjects may have needed a much longer time to evaluate target stimuli in the count condition than in the reaction condition. Although the latency of P3b was prolonged in the count condition, the P3b amplitudes in the count condition were equivalent to those in the reaction condition. This may have been because the subjects could evaluate the target stimuli in the count condition as confidently as in the reaction condition (28). In fact, most of the subjects correctly remembered the number of target stimuli in the count condition.

Collectively, the target stimuli presented in the count conditions may be processed with the same degree of attentional resources of subjects as in the reaction condition. However, the 'speed-maximizing' instruction for the reaction condition (i.e., requirement of quick motor response) may provide the target stimuli with different stimulus meanings as compared with the counting instruction (i.e., conscious detection of target stimulus), resulting in shorter P3b latencies in the reaction condition compared with the count condition.

The present results of SSR showed that the target stimuli in the reaction condition evoked large SSR, whereas smaller SSR appeared in the count condition. The point of issue on SSR in the present experiment is which factor, target detection or motor production, is much more effective in evoking SSR. On the basis of the present results on P300, a primary difference between count and reaction condition seems to exist in the meanings of target stimuli presented in each condition. The stimulus meanings of the target stimuli may probably have arisen from the requirement for quick motor response, because the target detection factor existed in both conditions whereas the motor production factor existed only in the reaction condition. Likely stimulus meanings of the target stimuli are the attention (or arousal state) of the subjects, the speed-maximizing instruction given to the subjects, and movement of the subjects.

Regarding the attentional aspect of stimulus meaning, the present results of ERPs (N140 and P300) suggested that the subjects were much more attentive to the stimuli in the reaction condition than in the count condition, although the task complexity (involving memory load) in the count condition may be equivalent in the reaction condition. When a subject is attentive to stimuli, the ascending reticular activating system (ARAS) should enhance its activity, resulting in higher cortical arousal states (e.g., attention, consciousness, and awareness) of the subject (23). The arousal states of subjects are well known to primarily influence the elicitation of SSR (3, 25). The reason why the SSR became smaller in the count condition than in the reaction condition may be that the arousal level of the subjects was relatively lower in the count condition. In other words,

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† For example, under the feedback condition, the subjects were presented feedback signal (stimulus) delivering information about whether their responses to target signal were accurate or not.

the requirement of a motor response may enhance the arousal level as a 'preparatory state' of the subject in producing voluntary movements.

The speed-maximizing instruction (i.e., the requirement of quick motor response) given to subjects in the present experiment may provide the subjects with some additional stimulus meaning of the target stimuli. Siddle et al. (32) reported that when subjects quickly pressed a button, the SCRs that appeared were twice as large as those when the subjects did not press the button. Siddle et al. suggested that the stimulus significance (which is identical to the 'stimulus meaning' 17) is an important determinant of EDA. Bernstein and Taylor (6) also showed that SCRs appeared larger for a pedal-pressing response to given stimuli than for non-relevant stimuli. With reference to the findings of SCR (such as the findings of both Siddle et al. and Bernstein & Taylor), Roth (30) suggested that the 'signal value' (which is identical to 'stimulus value' as one of the variables of stimulus meaning, 17) as well as subjects' attention directed to given tasks (i.e., requirement of motor response) affects both the EDAs (e.g., SCR) and P300. On the basis of both the findings of SCR studies and the present results, it is suggested that the requirement of quick motor response provides subjects with a particular meaning of the target stimuli, resulting in shortened P300 latencies and enhanced SSR amplitudes in the reaction condition, as observed in the present experiment.

The third likely meaning of target stimuli in the present experiment is the production of voluntary movements, which directly influenced the SSR. Osada et al. (26) reported that SSR rose together with the bereitschaftspotential (20) and the event-related desynchronization (ERD) of EEG-alpha waves (27) preceding self-paced voluntary movements, suggesting that information-processing relating to motor preparation affected the elicitation of SSR. The findings of Osada et al. (26) indicate that activation of the brain regions (e.g., the primary and supplementary motor areas) in programming motor command for a voluntary movements (8, 35) also activates the autonomic responses. Moreover, Sequeira and Roy (31) showed that electrical stimulation at the pericruciate area (corresponding to the primary and supplementary motor areas in humans) of the cat elicited larger skin potential responses (a type of EDAs) compared with those caused by stimulation at the parietal area (the somatosensory areas in humans). Although there are few data directly supporting this possibility in humans, it is likely that movement-related information processing enhances autonomic nerve activity. This should need to be further examined in future research.

In conclusion, the stimulus meanings, that is, the arousal states of subjects, speed-maximizing instruction, and movement-related information-processing, specific to the target stimuli given in the reaction condition (where the subjects were asked to respond by motor production), are much more effective in evoking SSR than the stimulus meanings requiring target detection in the count condition. In other words, motor production may enhance both the arousal state and the stimulus meaning which relates to the voluntary movement itself, and then activates the autonomic responses. It is also suggested that the elicitation of SSR under both count and reaction conditions is mediated by task-relevant nature of the target stimuli. Nevertheless, information-processing for target detection per se plays still an important role in the elicitation of SSR, because the SSR in the count condition was also evoked by target stimuli (although it was smaller than that in the reaction condition) even when the subjects in the count condition were much less attentive to the stimuli.

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