The Relationship between the Sympathetic Skin Response and Event-Related Brain Potentials in Sensorimotor Control of Human Voluntary Movements

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感覚－運動系の随意運動制御における交感神経皮膚反応と事象関連電位の関係（英文）

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THE RELATIONSHIP BETWEEN THE SYMPATHETIC SKIN RESPONSE AND EVENT-RELATED BRAIN POTENTIALS IN SENSORIMOTOR CONTROL OF HUMAN VOLUNTARY MOVEMENTS

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This thesis describes original research carried out by the author whilst enrolled in the doctoral program in the Graduate School of Science at the Tokyo Metropolitan University from April 1996 to May 1998. The experiments reported in this thesis were conducted by the author at the Institute of Health and Sport Science of the University of Tsukuba.

M. Shimoda
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The autonomic nervous system (ANS) maintains the internal environment of the human body. It has recently been suggested that the ANS also contributes to the control of voluntary movements. Especially, the sympathetic nervous system in the ANS plays an important role in subserving voluntary movements. Many researchers have become to be interested in the neuro-behavioral relationship between the ANS and the cortical motor areas, such as the primary motor area, supplementary motor area, and cingulate motor areas. However, this issue has not yet been well examined.

Sympathetic skin response (SSR) is a type of the electrodermal activity (EDA), which reflects electrical activity of the sweat glands in the skin. The SSR is usually used as an index of activation of the SNS, which controls the activity of the sweat glands. The SSR appears when a stimulus is presented without any anticipation for the stimulus, therefore suggesting that the SSR is a manifestation of orienting response (OR) of the ANS. The orienting response (OR) is made through a series of processes that one’s attention is automatically attracted to a startling (or novel) stimulus and that the content or information conveyed by the stimulus is then analyzed. Such a type of information processing is called the automatic mode of information processing. These facts suggest that the SSR (and EDAs) occurs when a given stimulus is involuntarily processed in the automatic mode of information processing.

The EDAs including SSR have also been suggested to appear when one is required to respond to a given stimulus. Given that the performers have to pay attention to the stimulus in order to do a particular response, the given stimulus is assumed to have the task relevance. Information processing of this type of stimulus is called the controlled mode of information processing. Therefore, it is likely that the SSR is also mediated by the controlled mode of information processing.

Event-related brain potentials (ERPs) are used to investigate information processing in the sensory-motor system of the brain. A P300 component of the ERPs is used to evaluate the higher brain functions such as cognition, decision-making, discrimination, etc. The P300 component has two sub-types, P3a (or novelty P3) and P3b. P3a (or novelty P3) is suggested to reflect that a given stimulus is processed in the automatic mode of information processing, while the P3b is to reflect that a given stimulus
is processed in the controlled mode. Accordingly, the neuro-behavioral relationship between the SNS and the sensory-motor system can be examined using dual-recordings of both the SSR and ERPs.

In the present study, the relationship between the SNS and the voluntary movement was examined from the viewpoint of information processing in the sensory-motor system, by means of the dual recording of both SSR and ERPs.

Experiment 1 examined whether the SSR is mediated equally by both the two modes of information processing, that is, the automatic mode and the controlled mode of information processing. In the present experiment, two types of rare stimulus, that is, target and nontarget, and frequent standard stimulus were presented to subjects. Subjects were asked to respond to the target stimulus by movement production and to ignore to both the nontarget and standard stimuli. In such a three-stimulus paradigm, it was assumed that the nontarget stimulus was processed in the automatic mode, and the target stimulus was processed in the controlled mode. Results showed that the amplitudes of both SSR and P300 (i.e., P3b) were larger for the target stimuli than those for the nontarget stimuli. P3a (or novelty P3) was not evoked by either rare stimulus. Therefore, it was suggested that the SSR might arise when a given stimulus was processed in the controlled, rather than the automatic, mode of information processing.

The results of Experiment 1 suggested that the SSR is primarily mediated by the controlled mode of information processing. The controlled mode of information processing is also activated during voluntary movements as a response to task-relevant stimuli. The task-relevant stimulus means a stimulus which requires subjects to both consciously detect the target stimulus and respond to it by movement production. Some previous studies have conducted experiments in which subjects were asked to respond by performing a voluntary movement to target stimuli, suggesting that the EDAs fluctuate when the subjects detected given target stimuli. However, in these studies, factors relating to voluntary movement have not yet been examined. In Experiment 2, the effectiveness of voluntary movement on elicitation of SSR was therefore examined under two conditions. In one condition (Count condition), subjects were asked to detect target stimuli, while in the other condition (Reaction condition), they were asked to respond by performing an arm movement to each target stimulus. Main results of Experiment 2 showed that the amplitudes of SSR occurring at the target stimuli were larger in the Reaction condition than in the Count condition and that the amplitudes of P300 did not differ between both
Abstract

conditions. It was therefore suggested that the elicitation of SSR was affected by some factors relating to the production of voluntary movement.

Movement production may be mediated by information processing for evaluating given stimuli (i.e., stimulus evaluation processes) as well as for producing motor responses (i.e., movement-related processes). The two processes are suggested to progress in serial in the sensory-motor system of the brain. In a reaction-time experiment, when a warning stimulus (WS) is given to subject prior to the appearance of imperative stimulus (IS) to which the subject are asked to respond, both the latency of P300 and the reaction time usually shorten. This is because subjects can anticipate the forthcoming IS and make a preparation for the desired motor response, resulting in quick processing of stimulus evaluation. In Experiment 3, the stimulus evaluation processes of a given stimulus was manipulated by either the presentation (i.e., WS-IS condition) or withdrawal of WS (i.e., Oddball condition), and then SSR for the IS was examined. Results showed that the latencies of P300 for the IS were shorter under the WS-IS condition than those under the Oddball condition, while the amplitudes of SSR for the IS did not differ between both conditions. It was therefore suggested that the SSR was not affected by the presentation of WS.

Because of findings of Experiment 3, the SSR was suggested to relate to the movement-related processes. In such movement-related processes, various regions of the brain, such as the primary and supplementary motor areas and cingulate motor area, are suggested to be activated. Activities of these brain regions differ between when subjects perform movements and when the subjects avoid the execution of movements. The brain regions are also suggested to control of activities of the sweat glands (e.g., SSR), because the regions have direct neural connections with the limbic system, which plays an important role in controlling the autonomic nervous system. In Experiment 4, the SSR and P300 were examined by means of a paradigm in which two types of target stimulus, that is, Go and NoGo stimuli, were presented to require subjects to either produce or avoid the desired movements. Results showed that both the latencies and the scalp distribution of P300 did not differ for the Go and NoGo stimuli, while the amplitudes of SSR for the Go stimuli was larger than those for the NoGo stimuli. Furthermore, a negative deflection of ERPs appeared, indicating activation of the brain regions arising in the processes of movement inhibition. Therefore, it was suggested that the SSR was enhanced when subjects actually perform movements, while the SSR was rather suppressed when subjects
Abstract

have to avoid the execution of a prepared movement.

In conclusion, the main findings in the present study are that the SSR is mediated by the controlled mode of information processing (Experiment 1) and is affected by voluntary movements (Experiment 2). Regarding factors relevant to voluntary movement, the movement production per se, rather than the stimulus evaluation, as well as the neural activities in various movement-related brain regions should be suggested to affect the SSR elicitation (Experiments 3 and 4). Furthermore, all the experiments conducted in this study clearly demonstrated significance of the dual recordings of ERP and SSR in examining the behavioral functions of cortical and sympathetic nerve activities in sensorimotor control of human voluntary movement.
CHAPTER 1 INTRODUCTION

1.1 THE AUTONOMIC AND CENTRAL NERVOUS SYSTEMS

In our daily life, humans always maintain a certain relationship between themselves and the surrounding environment, which must be cooperative for successful human behavior. Various human behaviors necessarily include responses which are physiological (such as blood circulation, respiration, and regulation of body temperature), instinctive or emotional (e.g., feeding, sleeping, sexual behavior, fear, rage, motivation), and psychological (e.g., learning, memorization, judgment, thinking, discrimination). In general, the term human behavior does not mean the functions of specific cells and/or organs but rather means the integrative interaction with the environment. Irrespective of the microscopic or macroscopic point of view, human behavior is a type of communication between humans and their environment.

The environment surrounding the humans is generally categorized into the internal and external environment. In brief, the internal environment (i.e., the internal milieu) means the physiological states of circulatory, respiratory, digestive, and metabolic systems of the human body. The external environment (i.e., the external milieu) includes the physical (e.g., atmospheric temperature, humidity, sound, light, vibration, hypoxia, smell, pain), biological (e.g., virus, bacterium, germ), and physiological (e.g., exercise) factors. Changes and conditions in both the internal and external milieu are detected by sensory organs of the body. Various types of information about the internal and external environment are detected through sensory organs and input into the central nervous system (CNS), where information of various requisites for the humans to exist in the external environment is processed and integrated. Integrated information is used to make a plan or program producing a ‘goal-directed’ behavior, which meets our instincts and the environmental requisites. Most human behavior, particularly goal-directed behavior, is necessarily subjected to the plan or program, and is produced more or less by ‘voluntary’ movements with the intervention of muscular contraction. The functions of transmitting/integrating information and making behavioral programs as well as activating the sensory organs and the muscles are all mediated by the nervous system. That is, the nervous system of the human body has essential roles for human behavior.

The nervous system of the human body consists of the central and peripheral
nervous systems, which include the somatic and autonomic nervous systems. The autonomic nervous system (ANS), composed of two sub-systems (the sympathetic and parasympathetic nervous system), controls the autonomic functions, such as cardiovascular and digestive functions, through the cooperation of the two sub-systems (see Chapter 2). The ANS is considered to be closely related with unconscious and involuntary functions of the body and is therefore often called the vegetative system. The somatic nervous system controls both motor and sensory activities and primarily mediates conscious and voluntary functions.

A fundamental function of the ANS is to maintain the internal milieu of the human body, that is, the homeostasis (Cannon, 1929), and is in general automatically controlled in a reflex form by the brainstem and the hypothalamus (e.g., Hess, 1954). Furthermore, it has recently been suggested that the functions of brain structures higher than the hypothalamus, such as the limbic region, neocortex, and cerebellum, are also important for the ANS activities. The limbic regions including the hypothalamus have direct neural connections with the primary (MI) and supplementary motor areas (SMA) through the cingulate motor cortex, which are all characterized as having important roles in producing movement. Furthermore, it has already been shown (Barker & Saito, 1981; Saito et al., 1990) that, during voluntary movements, the activities of the sympathetic nerves innervating the relevant skeletal muscles are controlled by central neural commands. Such sympathetic activities increase the blood flow to supply oxygen for the relevant muscles, thus subserving the production of goal-directed behavior by maintaining the homeostasis. These findings suggest that the neurophysiological functions and neural structures of the ANS are closely related with those of the CNS. Koizumi and Brooks (1972) have stated that "the central nervous system controls both autonomic and somatic responses and relates them as needed to effect a specific purpose."

However, likely neuro-behavioral relationships between the ANS and CNS have not yet been well examined. To examine the behavioral functions of the ANS, the electrodermal activity (EDA) has been used as a measure of the activities of the ANS. The EDA reflects electrical excitation of the sweat glands in the skin, which is evoked by activation of the sympathetic nervous system. In studies of human behavior, relationships between the EDA and orienting response (OR) have been focussed upon. The OR is a series of processes in which the individual's attention is automatically attracted to a startling (or novel) stimulus and the content or information conveyed by the stimulus is
then analyzed (Sokolov, 1963). Such a type of information processing is called the 'automatic mode' of information processing (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977). Since the EDA occurs with the OR, it has been suggested that the EDA appears when a given stimulus is involuntarily processed in the automatic mode (Lagopoulos et al., 1997; Lagopoulos et al., 1998). Namely, the EDA has a relationship with the automatic mode of information processing.

The EDA also appears when one is required to respond to a given stimulus (Siddle et al., 1979; Woestenburg et al., 1981; Woestenburg et al., 1983). Given that the performers have to pay attention to the stimulus in order to make a particular response, the given stimulus is assumed to have task relevance. Information processing of this type of stimulus is voluntary, being called the 'controlled mode' of information processing (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977). Therefore, the controlled mode differs from the automatic mode in terms of the requisite for attention (Imanaka et al., 1993). Collectively, it is also likely that the EDA has some relationships with the controlled mode of information processing. However, this notion has not yet been widely accepted.

Furthermore, a relationship between the EDA and voluntary movement is also suggested to exist (Siddle et al., 1979). It has already been shown that reaction movements to a given stimulus are performed faster when the arousal level (or consciousness) of performers is higher, which reflects on the enhancement of EDA (Freeman, 1940), and that performers who show a high activation level of spontaneous EDAs tend to respond faster with short reaction times (RT) than those who show a low activation level of EDAs (Surwillo & Quilter, 1965).

The reaction time (RT) reflects the total time spent for information processing during the interval from the onset of a given stimulus to the production of a motor response. The nature of information processing in the sensory-motor system of the brain has recently been investigated in detail by recording the event-related potentials (ERPs) on the human scalp. It is suggested that the ERPs consist of various components corresponding to various stages of information processing, such as identification of the stimulus, judgment, decision-making, and execution of response (Tadai et al., 1986). For example, the appearance of the P300 component of ERPs signals the completion of information processing of a given stimulus. Subcomponents of the P300, that is, P3a/Novelty P3 and P3b, are suggested to correlate with the automatic and controlled...
modes of information processing, respectively (Squires et al., 1975b). Accordingly, the neuro-behavioral relationships between the ANS and CNS can be examined using dual-recordings of both the EDA and ERPs.

Some researchers have investigated the behavioral functions of the ANS for human behavior using dual-recordings of both EDA and ERPs. Roth (1983) suggested that cortical (i.e., P300) and sympathetic (i.e., EDA) activities may be related with some or all of the processes of a given stimulus, and that such processing (i.e., automatic processing) was associated with the processing of an orienting response (OR). Recent studies (Miyakawa et al., 1992; Deguchi et al., 1996; Ito et al., 1996; Knight, 1996; Lagopoulos et al., 1997) have further shown that the sympathetic skin response (SSR), a type of EDAs, appears with P3a and/or Novelty P3, suggesting that the EDAs are the manifestations of OR in the autonomic nervous system.

In contrast, Osada et al. (1998a) have shown that SSR appears with the P250 component of ERPs when the performer voluntarily responds to a given stimulus. The P250 component is suggested to indicate the attentional state (or awareness) of the performer (Hatakeyama et al., 1998b; Hatakeyama et al., 1998a). Osada et al. have therefore suggested that the SSR (i.e., EDA) is affected by subjects’ attention. Furthermore, Aihara et al. (1998) have also shown that the SSR appears when subjects voluntarily produce a movement at their own pace. In the light of the fact (Sequeira & Roy, 1993) that electrical stimulations at the motor cortex in the cat invoke the EDA responses with muscular contraction, the findings of Osada et al. and Aihara et al. suggest that sympathetic nerve activities are mediated by movement production. However, this issue has not yet been sufficiently examined.

On the basis of the recent findings regarding the SSR and ERPs, the present study further examined the relationship between sympathetic nerve activity and voluntary movement from the viewpoint of information processing in the sensory-motor system, by means of the dual-recording of both SSR and ERPs.

In Experiment 1, the relationship between the two modes of information processing and the sympathetic nerve activity (i.e., SSR) was examined. As suggested by Roth (1983), both the automatic and controlled information processing in the sensory-motor system and EDA are influenced by the nature of a given stimulus. Especially, a novel stimulus is processed in the automatic mode and invokes EDAs which are characterized as the OR (Miyakawa et al., 1992; Deguchi et al., 1996; Ito et al., 1996;
Knight, 1996). In contrast, the stimulus nature of task relevance may also affect the EDAs (Siddle et al., 1979; Woestenburg et al., 1981; Woestenburg et al., 1983). Human behavior is inherently characterized by 'goal-directed' voluntary movements, which are often performed in response to a task-relevant stimulus. Such a task-relevant stimulus is processed in the controlled mode of information processing. Therefore, it is likely that the EDAs are also mediated by the controlled mode of information processing for the task-relevant stimulus. In Experiment 1, both the automatic and controlled modes of information processing were identified by means of ERPs and the changes in SSR corresponding to the two modes of information processing were then examined.

In Experiment 2, the effectiveness of a task-relevant stimulus (processed in the controlled mode) on the sympathetic nerve activity (SSR) was examined. Generally, in studies of P300, subjects are asked to either detect or respond to a target stimulus. This means that the target stimulus should have two types of task relevance, that is, conscious detection and movement production. Both are suggested to enhance the amplitude of P300 (Johnson, 1988a). However, it has not yet been investigated which of conscious detection or movement production is more effective in evoking the sympathetic nerve activity (i.e., SSR). Therefore, Experiment 2 examined this issue.

In Experiment 3, the relationship between the two activities, that is, the sensory-motor activity and sympathetic nerve activity (SSR), in information processing was examined. Information processing in the sensory-motor system includes the stimulus evaluation (or stimulus processing) and movement preparation (or response). The stimulus evaluation processes consist of stimulus identification, decision-making, and context updating (i.e., updating the memory of a given stimulus after the evaluation of incoming information on the stimulus). The movement-related processes consist of response selection, response programming, and response execution (Hiramatsu et al., 1985a; Tadai et al., 1986). The P300 reflects the stimulus evaluation processes alone, while the reaction time (RT) should be mediated by both processes (Kutas et al., 1977; Pfefferbaum et al., 1983; Tadai et al., 1986). In a reaction-time experiment, when a warning stimulus is presented prior to the imperative stimulus to which the subjects are asked to respond, both the latency of P300 and RT of the subjects shorten. This suggests that the warning stimulus affects the stimulus evaluation processes. However, it has not yet been examined whether or not the presentation of a warning stimulus influences the sympathetic nerve activity (i.e., SSR). In Experiment 3, the stimulus evaluation processes of a given stimulus...
were manipulated by either the presentation or withdrawal of a warning stimulus, and then the SSR for the stimulus was examined.

Furthermore, in Experiment 4, the effect of activation of the movement-related processes on sympathetic nerve activity (SSR) was examined. Voluntary movements were produced by activating the movement-related processes in various brain regions, such as the MI, SMA, and cingulate motor cortex. It has recently been suggested that the movement-related brain regions are also activated with the control of EDA (Sequeira & Roy, 1993, see Chapter 2; Devinski et al., 1995; Fredrikson et al., 1998). Therefore, it is predicted that the activation of these brain regions also affect the SSR during the production of motor activities. In Experiment 4, this prediction was examined by means of a paradigm in which two types of stimulus, that is, Go and NoGo stimuli, were presented to require the subjects to either produce or avoid the desired movements.

In the conclusion of this section, to investigate the relationship between the ANS and CNS during the production of voluntary movements, we conducted four experiments examining the effects on SSR of i) the automatic and controlled processing, ii) conscious detection and movement production, iii) the stimulus evaluation and movement-related processes, and iv) the effectiveness of movement-related brain activities. The rationale and details of each experiment are described in Chapter 3.

1.2 TERMINOLOGY

1.2.1 EMOTIONAL SWEATING

Emotional sweating is the increment of perspiration in the sweat glands with psychological excitation and emotional stimulation. Activation of the sweat glands refers to the electrodermal activity.

1.2.2 ELECTRODERMAL ACTIVITY (EDA)

Electrical activity of the skin occurring with emotional sweating. There are two basic methods for the measurement of EDA: the recording of skin conductance (SC) and skin potential (SP). Both activities are mediated by the same afferent and efferent pathways, with the difference being only in the mode of measurement. The SC is recorded through bipolar electrodes and SP is recorded with a unipolar arrangement.
1.2.3 Orienting Response (OR)

The orienting response (OR) was first discovered by Pavlov (1927) as a reflex elicited by an environmental change. The biological significance of the OR is to let the organism turn toward the source of stimulation in order to analyze its content or meaning (Sokolov, 1963).

1.2.4 Sympathetic Skin Response (SSR)

Sympathetic skin response, which is a type of SP, appears as the response to a startling stimulus. The SSR has previously been described in the literature (Shahani et al., 1984) on sudomotor sympathetic functions using a simple and non-invasive test (see later Section 2.1.4).

1.2.5 Event-Related Brain Potentials (ERPs)

The event-related brain potentials (ERPs), recorded on the scalp, are suggested to be related with various psychological and physiological events of information processing occurring in the brain structure (see later Section 2.2.2).

1.2.6 N140

A negative component of ERPs peaking at about 140 msec after the onset of a given stimulus. The N140 is suggested to be sensitive to the attentional state of the subject (see later Section 2.2.2.1).

1.2.7 P300

A positive component of ERPs peaking at about 300 msec after the onset of a given stimulus. The P300 often appears as the third positive deflection after the stimulus presentation, being called the P3. The P300 is recorded from the scalp in the visual, auditory, and somatosensory stimulations. In contrast to the early component of the ERPs (e.g., N140), it has been shown that the scalp distribution of P300 reveals no substantial differences among the three modalities (i.e., visual, auditory, and somatosensory, Snyder et al., 1980). The P300 is generally recorded using a version of the 'oddball paradigm' (see later Section 2.2.2.2).
1.3 LIMITATIONS OF THIS STUDY

The experimental results of this study are subjected to the following methodological limitations.

1.3.1 SYMPATHETIC INNERVATION

Sympathetic nerves innervate the skin, muscle, and other visceral organs. The sympathetic nerves in the skin innervate both the sweat glands and vessels (Hagbarth et al., 1972). Two components, sudomotor and vasomotor, work independently of each other (Arunodaya & Taly, 1995). Therefore, the SSR is limited to relate to the sudomotor component of skin sympathetic nerve activity alone.

1.3.2 AVERAGING METHOD

In this study, the averaging method was used to examine changes in both sympathetic (SSR) and cortical activities (i.e., ERPs). Using this method, it is possible to extract physiological phenomena repeatedly elicited with a particular event, such as the onset of EMG, given signal/stimulus, from the raw electrical potentials, by canceling noise components which are not synchronized with the event. This method is therefore usually used for recording ERPs.

However, there is some disadvantage to this method. First, the SSR tends to be subjected to habituation phenomena. Namely, SSR becomes weaker with an increase in number of repetitions of the presentation of a particular stimulus, because of habituation gradually developed through a long-term experiment (Mimori & Tanaka, 1992; Arunodaya & Taly, 1995). In attempting to avoid such a habituation phenomenon, particularly in clinical diagnosis, each SSR waveform is often examined (Shahani et al., 1984; Yokota et al., 1993a; Yokota et al., 1993b; Rousseaux et al., 1996). Otherwise, the largest four (Andary et al., 1993) or five (Watahiki, 1987a; Baba et al., 1988) SSR waveforms are selected from all the SSR recordings obtained under a given condition to be examined.

As another likely disadvantage, the averaging method needs many trial data to be averaged under a certain condition. This means that the participants are usually asked to repeatedly perform the desired task, with their arousal and attention being maintained at a certain level. Therefore, the experimenter should consider both whether or not the time length of experiments is too long for the subjects and also whether or not the number of trials is large enough to obtain a significant waveform or not.
In spite of those disadvantages of the averaging method, Aramaki et al. (1997) have recommended an alternative averaging method which is useful in recording the SSR without causing habituation phenomena. In his 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 the subjects were asked to ignore, are presented at a high probability (e.g., 80%). Using this sequence, the SSR wave constantly appears with the target stimuli. This method is the same as the stimulation sequence used for the ‘oddball paradigm’ which is a typical paradigm to record the P300. In fact, some studies of SSR have used the averaging method with target and standard stimuli, such as those used in the oddball paradigm (Deguchi et al., 1996; Ito et al., 1996; Knight, 1996). This type of averaging method was also used in all the experiments of this study to record both SSR and ERPs.

Another limitation existing in the averaging method is as follows. Any meaningful signals embedded in a single trial can not be detected by the averaging method. Mimori and Tanaka (1992) have suggested that if the experimenter uses the averaging method to evaluate SSR waves, it could fail to pick up in each single trial some meaningful, but temporary phasic activity in the sympathetic nervous system. Such a limitation has often been discussed in studies on ERPs using the averaging method. Although some researchers (Ritter et al., 1979; Hiramatsu et al., 1985b; Ito, 1993) have attempted to analyze the P300 by examining each single waveform, a number of researchers have still used the traditional averaging method, because of difficulties in using the single-trial analysis of ERPs. In the present study, because both the SSR and ERPs should be recorded at the same time, the traditional averaging method was used.

1.3.3 Subjects

Neurological studies on ERPs and SSR have often used experimental animals or patients with neurological disorders, in order to discuss (a) possible neural network(s) corresponding to elicitation of both responses (i.e., ERPs and SSR). In contrast, the experiments conducted in this study used healthy adult volunteers as subjects. This is because the subjects were required to correctly understand the given stimuli and to perform the required reaction time (RT) tasks.
1.3.4 Emotions of Subjects

It is plausible that the stimulus to which the subjects are asked to perform a motor response could activate emotional states of the subjects, such as happiness, surprise, anger, fear, sadness and disgust. The activation of autonomic responses underlying such emotions has often been investigated (e.g., Collet et al., 1997, see also Chapter 2). In this study, although the emotions of subjects were not manipulated during the experiments, the subjects were instructed to keep their emotion stable. Therefore, the effect of emotions on SSR was not discussed in this study, on the assumption that the emotional conditions of the subjects were constant during the experiments.

1.4 Significance of this Study

As previously mentioned (see Section 1.1), the relationships between information processing in the sensory-motor system and autonomic nerve activities during voluntary movements have not yet been fully investigated. In the present study, SSR and ERPs were simultaneously recorded as indices of the two systems (i.e., sympathetic and cortical) under various task conditions in which subjects were asked to perform a voluntary movement. This enables us to discuss both the sensory-motor system of the brain during voluntary movements and changes in the sympathetic nerve activities corresponding to movement production.

Furthermore, all the experiments conducted in the present study clearly demonstrate a methodological significance of dual recordings of both ERPs and SSRs for the investigation and evaluation of the roles of cortical and sympathetic nerve activities.
CHAPTER 2 REVIEW OF LITERATURE

2.1 SYMPATHETIC NERVOUS SYSTEM AND ELECTRODERMAL ACTIVITY

Sympathetic skin response (SSR) is one type of the electrodermal activity (EDA) and is used as an index of activities of the sympathetic nervous system. The sympathetic nervous system (SNS) is one of the sub-systems of autonomic nervous system (ANS). Another sub-system is called the parasympathetic nervous system (PNS). The two sub-systems differ in several points. First, neuro-anatomical distributions of the nerve fibers differ for the two sub-systems (i.e., SNS and PNS). The sympathetic nerves originate in the spinal cord, whereas the parasympathetic nerves originate mainly in the tenth cranial nerve, which is the vagus nerve. Second, the nature of stimulatory effects of the two sub-systems on effector organs is often antagonistic to each other. Third, the types of hormonal transmitter substances secreted at nerve endings are usually different between the two systems, with some exceptions. These differences between the SNS and PNS are closely described in a number of textbooks on physiology (e.g., Ciriello et al., 1986; Ganong, 1991). The details of them are therefore not described in this chapter. In the following section, an overview of the EDA is first examined and the literature on the neurophysiological correlates of EDA is then reviewed.

2.1.1 EMOTIONAL SWEATING AND ELECTRODERMAL ACTIVITY

Sympathetic impulses originating from the central nervous system (CNS) are delivered to the sweat glands in the skin. This causes ‘emotional sweating.’ This phenomenon is seen as an electric activity of the skin. Charles Féré, a French neurologist, reported in 1888 the observation that the changes in electric activity of the skin can be enhanced by various physical and emotional stimuli. In 1890, a Russian physiologist, Tarchanoff, observed similar electrical changes in the skin.

The techniques used by the two scientists differed to each other. Féré’s procedures involved the loading of weak electric current between two electrodes on the skin surface. This method enabled the EDA to appear when a person was provided with various stimuli. In this method, a galvanometer was used to measure skin conductance changing when a visual or auditory emotion-provoked stimulus was presented. This phenomenon was named the psychogalvanic reflex (PGR) and was later called the galvanic
skin response (GSR). Féré concluded, on the basis of his findings, that the responses indicated the excitation of central nervous system, or "arousal."

In contrast, Tarchanoff measured electric potential rather than conductance to examine galvanometer deflections similar to the Féré's findings, without any loading of electric current. Electric potential of the skin normally changes whenever subjects are stimulated with any stimulation. Both Féré and Tarchanoff thus contributed to establishing the basic methods for measuring EDA, that is, the skin conductance (SC) and skin potential (SP).

An interesting aspect of these sweating phenomena is that this is not only thermoregulatory but also emotional. This fact developed the basis of research strategies used for examining behavioral phenomena. Sweating, or sweat gland activity, can be observed as a change in SP and SC in a variety of situations, such as those that emotionally arise. For example, the eccrine glands in the palms and fingers of the hand respond strongly to psychological and sensory stimuli but only weakly respond to heat. We often experience wet or 'clammy' palms in the conditions of fear or anxiety but not in warm conditions. The sweating with psychological stimuli is sometimes termed 'arousal' sweating, and some researchers believe it is adaptive. Darrow (1933) suggested that the sweating of palms and soles may be an adaptive response that have persisted over the course of evolution and that it aided in grasping objects, such as a weapon in a fight and branches of trees during flight, and etc. Wilcott (1967) assumed that the arousal sweating in any part of the body may cover the skin so as to protect it from mechanical injury. Suggestion by Edelberg (1972) is that sweat gland activities may decrease the body temperature in emergency situations that require a great deal of physical effort (e.g., running or fighting). According to these notions, the sweat gland activity may be characterized as adaptive functions of body efficiency in emergency.

### 2.1.2 Neural Control of the Electrodermal Activity

To investigate physiological functions of emotional sweating (i.e., EDA), neural mechanisms of EDA should be examined. Both a number of psychophysicists and neurologists have discussed the neural mechanisms of EDA, concluding that the EDA is controlled by both excitatory and inhibitory mechanisms which probably act upon autonomic neurons, such as sympathetic preganglionic neurons, in the spinal cord. The neural structures responsible for controlling the EDA are the spinal cord, reticular
formation, hypothalamus, limbic system, and cerebral cortex of the brain.

2.1.2.1 Spinal and reticular control of the electrodermal activity

The systems controlling the EDA in the lower level of CNS are located in the spinal cord and reticular formation in the brain stem. At the spinal level, the sudomotor neurons are influenced by excitatory and inhibitory impulses from the supraspinal centers, such as the reticular formation, hypothalamus, limbic system, and cerebral cortex. In fact, when the spinal cord is injured, sweating of the skin temporarily becomes inactive. Moreover, the sweat glands receive only the sympathetic innervation. The spinal neurons are therefore considered as a primary 'final common pathway' for the control of sweating, although the ganglionic neurons are the actual final controlling neurons (Roy et al., 1993).

The supraspinal mechanisms responsible for controlling the EDA may be the reticular formation of the brain stem. Although the reticular formation has been thought to influence the cerebral cortex to increase the arousal level (e.g., Moruzzi & Magoun, 1949), it is not seen anymore as a unitary non-specific arousal system. That is, many nuclei in the reticular formation mediate either specific excitatory or inhibitory functions of the EDA as well as motor and sensory neural activities (Wang, 1957).

A function mediating excitatory effects on EDA has been thought to exist in the brain stem. The reticular activation is linked with arousal of the cerebral cortex. EDAs arising with various stimulation are thought of as indices of excitability of the reticulo-cortical system. The intrareticular excitability changes according to various conditions, such as deep sleep and careful attention. Lindsley (1960) suggested that the ascending reticular activating system (ARAS), involving the pons, the mesencephalon, and the medulla, plays an important role in regulating neural conditions of attention, consciousness, sleep, and wakefulness. The Lindsley’s suggestion on the ARAS supports the activation theory (Freeman, 1940, see later) that describes the relationships between the levels of physiological activity and physical performance. It is therefore suggested that the ARAS activates the autonomic nerve activities.

In contrast, the medial ventral nuclei at bulbar inhibit the EDA (Wang, 1957). Wang (1958) described that, in anesthetized cats, the skin potential responses (SPRs) evoked by electric stimulation at cutaneous nerves were enhanced when the reticular formation became inactive by either cooling or a lesion of the medulla. It has been reported that SPRs mediated by reticular formation were also inhibited by stimulation of
the ventro-medial reticular formation (Yokota et al., 1963a).

Generally, the EDA is mediated by both the sympathetic nerve activities in the ANS and the reticular formation, which is thought of as a neural center controlling the autonomic activities. In addition, the hypothalamo-limbic structures also play an important role for autonomic activities. This is examined in the following section.

2.1.2.2 Hypothalamo-limbic control of the electrodermal activity

2.1.2.2.1 Hypothalamus

Since the classical research work of Hess (1954), the hypothalamus has been thought to be involved in controlling the autonomic system and thus to subserve the sympathetic control of both movements and emotional expressions. For example, when a monkey finds a natural enemy, the monkey would automatically do either fight with or run away from the enemy (i.e., 'fight or flight reaction,' Cannon, 1929). In such a situation, the ANS would be activated to increase both blood flow in musculature and sweating on palms and soles. This activation could enable the monkey to move quickly (i.e., fight behavior) or to jump away from one tree to another by hanging on a branch of trees (i.e., flight behavior). Karplus and Kreidle (1909, cited in Wang, 1964) demonstrated that stimulation at the 'tuber cinereum' (medial hypothalamus) in the cat caused sweating on the pads of all paws. Other early studies (Wang & Richter, 1928; Hasama, 1929) also demonstrated the hypothalamic activation arising with sweat gland activity. These findings indicated that the hypothalamus plays an important role in thermoregulation, thus mediating the EDA.

2.1.2.2.2 Limbic system

Showers and Crosby (1958) examined, using cats and monkeys, physiological mechanisms of the limbic system in relation to the EDA, showing that the cingulate gyrus mediates the control of sweating. Since then, a number of researchers (Yokota et al., 1963b; Lang et al., 1964; Kimble et al., 1965; Bagshaw & Benzies, 1968) have focussed on the EDA control and specific limbic regions, such as hippocampus, amygdala, and limbic cortex.

Regarding the hippocampus functions, Yokota et al. (1963b) examined non-anaesthetized curarized cats by stimulating the hippocampus, reporting inhibition of SPR (a type of EDA). This finding indicated an excitatory effect of the hippocampus on EDA.
Pribram and McGuiness (1975) examined habituation in EDAs using monkeys with hippocampectomy. In normal conditions, the EDA is gradually diminished when a stimulus is repeatedly presented. This is the habituation phenomenon in EDA. Pribram and McGuiness found less habituation in skin conductance responses (SCRs, a type of EDA) for the hippocampectomized monkeys, suggesting that the hippocampus had excitatory effects on EDAs. Furthermore, Hazlett et al. (1993) recently showed, using positron emission tomography (PET) to test schizophrenics, that the hippocampus facilitates EDA. However, Bagshaw et al. (1965) found that, using monkeys, bilateral lesions of the hippocampus did not influence the feature of EDA. Similarly, in humans, Tranel et al (1990) also showed that lesions at hippocampus in the limbic system did not affect SCRs. According to these findings, the effect of hippocampus activities on the EDA seems to be equivocal.

In contrast to the findings on hippocampus, the amygdala has generally been considered to have only an excitatory but not inhibitory influence on EDA. Lang et al. (1964) and Yokota et al. (1963b) showed that the stimulation at the amygdala produced SPRs in cats. Bagshaw et al. (1965) found that monkeys with bilateral amygdalectomy showed a decreased EDA to both frequent and novel tones, whereas normal monkeys showed habituation of EDA (measured by SPRs) to frequent tones but not to the novel tones. Similarly, Bagshaw and Benzies (1968), using monkeys, also found that the EDA normally arising with a surprising stimulus disappeared with bilateral amygdalectomy. These findings on animals all indicated that the amygdala has an excitatory effect on the EDA. In humans, Dallakyan et al. (1970) reported that the destruction of both the amygdala and the medio-basal parts of the temporal lobe resulted in an inhibition of SCRs, suggesting excitatory influences of amygdala on SCRs. Recently, Raine et al. (1991) showed, using a magnetic resonance image (MRI) technique, that large SCRs arising with orienting stimuli were significantly associated with a large area of left temporal/amygdala regions. Furthermore, a psychopathological study (Raine & Lencz, 1993) using schizophrenics supports, in part, the findings of the excitatory effect of amygdala on the EDA. These studies indicated the excitatory effects of amygdala on EDAs. In contrast to these findings, Tranel and his colleagues (Tranel & Damasio, 1989; Tranel et al., 1990) showed that patients “whose entire amygdaloid complex had been destroyed bilaterally” (1989, p.381) or patients showing “a bilateral mineralization of the amygdala, possibly including the amygdala-hippocampal transition area” (1990, p.350) generated normal
SCRs, indicating that the amygdala does not affect the EDA. This is inconsistent with the findings of excitatory influence of the amygdala on the EDA. Collectively, it is therefore concluded that the amygdala may have either excitatory or no effects on the EDA, at least in humans.

That the limbic cortex elicits SPRs was clearly shown by Isamat (1961). Isamat conducted experiments using direct electrical stimulation to the cortex, showing that SPRs were most easily evoked by the stimulation at the anterior limbic cortex, around and below the corpus callosum, and the infralimbic cortical areas. However, partial ablation of both the anterior cingulate cortex (a part of the limbic cortex) and the medial frontal cortex in the monkey (Kimble et al., 1965), and ablation of the anterior region of the limbic cortex in the cat (Wilcott, 1967) had no effects on EDA. Devinski et al. (1995) have recently summarized the functions of the anterior cingulate cortex. The anterior cingulate cortex is a large region around the rostrum of the corpus callosum. This is called the anterior executive region. This region has numerous neural projections into the primary and supplementary motor areas. However, these projections are suggested to originate from different parts of anterior cingulate cortex. Many studies (c.f., Devinski et al., 1995) have shown that the anterior executive region also has projections to large areas of the ANS, such as the amygdala and reticular formation. Therefore, the anterior executive region is assumed to mediate both ‘affect’ and ‘cognition’ functions. The affect functions of anterior cingulate cortex modulates both the autonomic activities and emotional responses to surprising or fearful stimuli (e.g., flight behavior), while the cognition function is engaged to the function of response selection associated with skeletomotor activities and responses to noxious stimuli (c.f., Devinski et al., 1995).

In conclusion, the hypothalamo-limbic system is thought to affect the EDA with both excitatory and inhibitory effects. Furthermore, recent neuroanatomical studies (c.f., Sequeira & Roy, 1993) have indicated that the limbic structure has close neural connections with the cerebral cortex. This suggests that neural/behavioral functions of the cerebral cortex are responsible for controlling the EDA in addition to those of the spinal cord, reticular formation, hypothalamus, and limbic system.

2.1.2.3 Cortical control of the electrodermal activity

We often experience that the heart rate (HR) increases before the onset of voluntary movements. When a person intends to perform a movement, various
physiological activities, such as HR, blood pressure, and sweating on the palm of the hands, normally increase prior to the movement. These phenomena indicate that the activation of cerebral cortex arising in preparation and anticipation of movements may well influence the autonomic activity (i.e., EDA) as well.

2.1.2.3.1 Frontal and non-frontal cortices

Studies on the influence of cortical activities on EDA have often examined both the excitatory and inhibitory effects of the frontal cortex. The frontal cortex, such as the motor and the supplementary motor areas (the pericruciate area, in cat), is thought of as the origin of motor programs used to elaborate goal-directed behaviors/movements. Darrow (1937) proposed a notion of close association between skeletomotor and sudomotor activities in the extremities. In this notion, the palmer sweating can be considered to protect skin from injury and to help performing a movement like grasping objects. Since Luria (1966) confirmed a facilitatory role of the frontal lobes in orienting activities, neural functions of the frontal cortex in the control of EDA have become interesting to many neurologists. Studies on the control of the EDA by the frontal cortex suggested that the frontal control is either excitatory (Wang & Lu, 1930; Wang & Mok, 1931; Spiegel & Hunsicker, 1936; Schwarz, 1937; Wilcott, 1969; Wilcott & Bradley, 1970), inhibitory (Guttman & List, 1928; Darrow, 1937; Wang & Brown, 1956; Sourek, 1965; Wilcott & Bradley, 1970) or non-influential (Shimizu et al., 1948; Elithorn et al., 1954; Kimble et al., 1965).

In order to clarify the effect of frontal cortex on the EDA control, Damasio et al. (1993, cited by Raine & Lencz, 1993) examined the influence of frontal cortex on SCRs, testing patients with bilateral lesions of orbital and mesial frontal cortex. Results showed that the patients (like normal people) produced normal SCRs to orienting stimuli of a loud handclap (which the patients could not anticipate). Damasio et al. therefore suggested that the frontal cortex might have no effects on the EDA. In contrast to Damasio et al., the effects of frontal lobes on EDA have been suggested to be excitatory. Raine and Lencz (1993) have examined the effects of cerebral cortex on the EDA, using several non-invasive imaging methods, such as computed tomography (CT), PET, and MRI, which are often used to detect lesions in the brain. Raine and Lencz have shown the prefrontal cortex to facilitate SCRs. On the basis of these studies, it can be concluded that the frontal lobes, particularly the orbital, insular and prefrontal cortex (Cechetto & Chen, 1990) predominantly influence EDAs.
It has also been suggested that the excitation of non-frontal areas in the brain affects the EDA. Early studies (Wang & Lu, 1930; Wang & Mok, 1931; Spiegel & Hunsicker, 1936) showed that SPRs were evoked by electrical stimulation at non-frontal areas, such as the posterior cruciate cortex and anterior suprasylvian areas, in cats. In humans, Dallakyan et al. (1970) showed that SCRs were suppressed when the medio-basal part of the temporal lobe was destroyed. Raine et al. (1991) suggested that the left temporal cortex (including the amygdala) is a source area of SCRs which is caused as a response to surprising stimuli. On the basis of these findings, various regions of non-frontal areas in the brain also seem to exert excitatory effects on EDAs.

There have been a number of studies suggesting tonic inhibitory effects of the cerebral cortex on the EDA. For example, Wilcott (1967) examined EDAs, using alerting stimuli, in normal cats and the cats with chronical ablation of the cortex. Ablations were made at sensori-motor areas, where some previous investigators had confirmed that EDAs were elicited by electric stimuli. The main results of Wilcott showed that the EDAs increased after the ablations. Wilcott explained the results in terms that an inhibitory effect of the cerebral cortex on EDA disappeared and that this inhibitory effect was tonic, instead of phasic in the excitatory effects of the cortex on EDAs. Accordingly, the cerebral cortex seems to exert both phasic excitatory and tonic inhibitory effects on the EDA.

2.1.2.3.2 Movement-related areas

A behavioral function of EDA in human is hypothesized to modify the cutaneous sensations that are useful for improving tactile acuity during fine motor control of the hands (Darrow, 1937; Edelberg, 1972). The pyramidal tract originating in the motor area of the cerebral cortex is the main efferent pathway to convey motor commands to the relevant musculature and is thus responsible for such fine motor control. It has also been suggested that artificial electric stimulation at this pathway could elicit both electrodermal responses and other autonomic responses (Langworthy & Richter, 1930; Landau, 1953). Sequeira and Roy (1993) have recently examined, using cats, whether the pericruciate cortex (in which the pyramidal tract fibers in the cat originate, Armand & Kuypers, 1980) could generate autonomic effences together with motor commands. The pericruciate areas of the cat correspond to the primary and supplementary motor areas and the somatosensory areas in humans. Sequeira and Roy tested the influence on EDA (i.e., SPR) of both the pericruciate and parietal areas. Results showed that the amplitudes of SPR elicited by stimulation at pericruciate areas were significantly larger than those evoked by
stimulation at parietal areas, suggesting that SPRs were more easily elicited by activation of pericruciate areas and that the activation threshold was lower for the primary motor area than the somatosensory areas. Sequeira and Roy further conducted a series of experiments and developed a technique of sectioning, called 'pyramidal preparation', with which all descending pathways except the pyramidal tracts were interrupted at bulbar level. This technique was used to interrupt pathways between the hypothalamus or reticular formation and the spinal cord. To ensure that the hypothalamo- and reticulo-spinal pathways were completely interrupted, a control stimulus was delivered to the hypothalamic and reticular structures before and after the pyramidal preparation. After the sections, neither the hypothalamic nor the reticular stimulation became to evoke SPRs. This means that both the hypothalamo- and reticulo-spinal pathways were completely interrupted. After the pyramidal preparation, the stimulation of the pericruciate cortex alone was shown to evoke SPRs with low thresholds. This finding also suggests that the excitation of motor cortex would generate EDAs together with motor responses. On the basis of these experiments, Sequeira and Roy concluded their findings with two main points. First, a direct phasic control of EDA can be exerted by the motor cortex through the pyramidal tract and this is independent of reticulospinal neurons. Second, the thresholds for eliciting SPRs after the bulbar transection are higher than those before the transection, suggesting a reticular amplification of the cortical excitatory effects on EDA under normal physiological conditions. Taking the main role of the reticular structures into consideration, it is believed that the cortico-reticulo-spinal circuit acts predominantly in the control of EDA under normal conditions (Sequeira & Roy, 1993).

In conclusion, it is suggested that autonomic efferences are amplified by the reticular formation and may also be affected by cortical motor commands through pyramidal tracts. The autonomic efferences then descend to the sweat glands through preganglionic sudomotor neurons in order to facilitate cutaneous adaptation (e.g., Darrow, 1937; Edelberg, 1972).

2.1.3 Behavioral Correlates of the Electrodermal Activity

The EDA is affected by various factors relating to the human behavior, especially orienting response (OR). The OR is suggested to be influenced by various properties of eliciting stimulus, such as stimulus novelty and stimulus significance. Stimulus novelty means the novel characteristics of a given stimulus differing from those of preceding stimulus, while stimulus significance means that particular significant information of a
given stimulus to be processed in the nervous system. These properties of the stimulus are thought of as critical factors affecting SSR (a type of EDAs). Therefore, the SSR is suggested to be a representation of OR in the ANS (Roth, 1983; Miyakawa et al., 1992; Deguchi et al., 1996; Knight, 1996; Lagopoulos et al., 1998). In the following part of this section, the literature on the OR is first reviewed in terms of elicitation of EDA and the another correlates (i.e., emotions and voluntary movements) of the OR are then examined.

2.1.3.1 Orienting response (OR)

The OR was first reported (Pavlov, 1927) as a reflex response automatically elicited by environmental change. Biological aim of the OR is to let the organism face toward the source of stimulation in order to analyze its content or meaning. Bodily manifestations of the OR are the lowering of sensory thresholds, dilation of pupil, quick movements of the eye and the whole body, fast rhythm of the EEG, and other various changes in autonomic function of the body. The most prominent change in autonomic function is seen as the EDA (i.e., SCR, SPR, and SSR), which occurs together with a variable pattern in HR, cephalic vasoconstriction, and finger vasodilation.

Many researchers (Berlyne, 1960; Sokolov, 1963; Kahneman, 1973; Wagner, 1976; Bernstein & Taylor, 1979; Maltzman, 1979; Öhman, 1979; Siddle et al., 1979) have examined behavioral significance of the OR and have become interested in a typical characteristic of the OR, that is, phenomenon of habituation. Habituation in OR is usually seen as a decrease in the amplitude of SCR, which gradually decreases as a stimulus is repeatedly presented to evoke OR. This habituation phenomenon of OR does not occur when either the intensity or duration of a given stimulus differs from that of the preceding stimulus. This is called dishabituation of OR.

2.1.3.1.1 Neuronal model

Sokolov (1963) suggested that the primary determinant of the OR was environmental uncertainty and proposed a theory of OR. According to Sokolov, incoming stimuli are compared with internal representations of past stimuli that are retained in the brain. When a stimulus is presented to a subject, he/she may feel that the stimulus is novel because this is a new experience for the subject. In such a situation, an OR appears with the stimulus. When such a stimulus is repeatedly presented, a “neuronal model” should be made in the brain as a perceptual representation of the stimulus. Each of the repeated stimuli may be compared with the neuronal model in the brain. When the stimulus
matches the model, the OR may well be gradually habituated. However, if a stimulus differed from the preceding stimulus in terms of its characteristic (e.g., intensity and duration of presentation), an internal representation of the stimulus would not match any existing “neuronal models.” Then, dishabituation of OR would appear. In the Sokolov’s theory, a match or mismatch between stimulus properties reflects the detection of novelty or stimulus change, and this is the critical factor in producing an OR.

Sokolov (1963) has further suggested that, in some situations, the OR is evoked only when the environment is characterized with high uncertainty. Such a high uncertainty in the environment may have information to be processed in the brain. It is therefore considered that the OR may play a role in information processing of the environmental stimuli. A number of western psychologists (e.g., Kahneman, 1973; Öhman, 1979) suggested that, in such situations, attention of a subject acts an important role in information processing in the brain.

2.1.3.1.2 Attention

According to Imanaka et al. (1993), the term attention has been actually used in the literature of experimental psychology in at least three different contexts, namely, (1) attention as alertness, (2) attention as selective attention, and (3) attention as a limited processing capacity. Alertness (arousal or consciousness, Öhman, 1979; Öhman et al., 1993) can be thought of as a state of the CNS being ‘ready’ to receive and process information at an optimal rate. According to the latter context (attention as a limited processing capacity), attention involves the problem of selecting only pertinent information for processing, and this aspect of attention is usually referred to as ‘selective’ attention. A theoretical model was proposed by Broadbent (1958) that selective attention was conceived to act like a filter allowing only a single channel of information to be processed, while blocking completely the processing of all other information.

An early study of Berlyne (1960) on attention suggested that attention had relation to arousal or alertness. He suggested that the characteristics of OR-eliciting stimulus, such as novelty, incongruity, and probability, were determinants which were important for phasic changes in subject’s arousal/alertness. Phasic changes in arousal level caused by given stimulus were assumed to be related to the enhancement of attention. Berlyne suggested that the enhancement of attention to the external environment as a whole raises the arousal level of a subject. He suggested that the OR was related to the enhanced
attention and that a large OR was produced by stimulus novelty, which made great demands on the information-processing capacity of the nervous system.

Kahneman (1973) has hypothesized that an OR reflects two types of information processing. One type of processes is a transient effort to process and analyze the eliciting stimulus. If a stimulus is detected as a novel or significant stimulus, the OR alters the allocation of attention. In such a situation, the attention of a subject is directed toward the stimulus so that the stimulus may be more efficiently processed. In his hypothesis, the attention or effort to process the given stimulus is seen to be purely involuntary. Kahneman has stated that the changes in allocation of attention due to control by higher neural centers should not be considered as ORs. Thus, the OR itself is not viewed to be mediated by cognitive intervention. However, both such a transient effort and the involuntary attention may compete for attentional capacity in the brain. Furthermore, changes in attentional allocation can be caused by instructions for subject to attend to given stimulus. Therefore, it also seems that the OR is mediated by voluntary and cognitive functions of the brain.

2.1.3.1.3 Stimulus significance

In contrast to the previous studies (Berlyne, 1960; Sokolov, 1963; Kahneman, 1973) on the OR, Bernstein and Taylor (1979) have suggested that significance of stimulus is a trigger for the OR. Bernstein and Taylor assumed two stages of information processing for analyzing the stimulus. In the early stage, uncertainty/novelty of incoming stimulus is detected by the subject and is then compared with a representation in the neuronal model which was hypothesized in the Sokolov's theory. In the later stage, significance of the stimulus is examined, resulting in elicitation of OR. Such the two-stage model of information processing predicts the absence of OR when a given stimulus is not evaluated as having any 'significance.'

To examine the Bernstein and Taylor's hypothesis, Siddle et al. (1979) have investigated the effect of stimulus significance on SCR in two types of reaction time (RT) experiments. In an experiment, male subjects received 12 trials with the presentation of a 5-sec, 1000 Hz tone and then a test trial with the tone of 500 Hz. A half of the subjects (RT group) were required to press a button as quickly as possible in response to the tone offset, while the other half (no-RT group) ignored the tones. In a second experiment, visual stimuli were used instead of the auditory tones. Male subjects received 12 trials
with the presentation of female names. As a following test trial, a half of the subjects (own-name group) were required to perform a rapid motor response to the presentation of their own name, while the other half (neutral-name group) received a male name which was neither their own nor that of their father, brother(s), close relatives or close friends. Results of both the experiments showed that the changes in both tone frequency (1000 Hz to 500 Hz) and name (female name to male name) solely elicited SCRs, suggesting that different characteristics of a given stimulus (i.e., tone frequency or name) can sufficiently elicit the OR (e.g., SCR). This is inconsistent with the Bernstein and Taylor's hypothesis (1979) that the OR occurs when a given stimulus is evaluated to have a particular significance. Furthermore, the RT and the own-name groups showed larger SCRs than the no-RT and the neutral-name groups. Siddle et al. concluded that the significance of a given stimulus was related to the elicitation of OR in addition to the stimulus novelty. Both Bernstein and Taylor and Siddle et al. suggested that the stimulus significance might affect the OR.

Furthermore, Maltzman (1979) has suggested that the significance of a given stimulus is induced by an instruction which is given by the experimenter to subjects. He thought that an OR was able to arise in response to a novel stimulus only under a particular state of the CNS (he called this particular state of the CNS "cortical set"), and that the particular state of the CNS influenced the nature of OR to the given stimulus. He then suggested that the particular state of the CNS might have a relatively short-lived characteristic which was induced by the experimenter's instructions, or it might have a long-standing characteristic which was necessary for evaluating the significance of the given stimulus.

Maltzman (1979) has also suggested that there are two types of OR. One type of OR simply occurs when a given stimulus differs from the preceding stimulus, as hypothesized in the Sokolov's OR theory. This has been called the involuntary OR. The other type of OR is mediated by cognitive activities of the brain when a given stimulus is evaluated to have a significance, as suggested by Bernstein and Taylor. This is called the voluntary OR.

2.1.3.1.4 Memory and information processing

Wagner (1976) has suggested that the OR appears when a given stimulus differs in either quantity or quality from the internal representation of a previously given stimulus.
which is stored in short-term memory (STM). In the theories of Sokolov (1963) and Maltzman (1979), the neuronal model or the cortical set is thought to be compared with the incoming stimulus. In this point of view, it is considered that the STM acts a role in information processing similar to the role of the neuronal model or the cortical set. Öhman (1979) has also suggested that an OR arises when a given stimulus differs from the memory representation of the preceding stimulus stored in the STM. Öhman has further suggested that such a stimulus may be processed in the controlled mode of information processing (see the next Section 2.1.3.1.5) and is then sent to the long-term memory (LTM). The LTM is then updated by the STM of the stimulus. When a given stimulus is similar to the preceding stimulus, the property of the given stimulus is consistent with the representation of the preceding stimulus in the STM. In such a situation, the OR may in all probability be inhibited.

2.1.3.1.5 Automatic and controlled modes of information processing

Schell et al. (1993) have proposed another model of OR which is explained in terms of memory and information processing in the brain. In their model, when a stimulus is presented to a subject, a complex series of information processing is executed. The early stage of information processing involves an automatic filtering process in which stimuli are compared to the representations in the STM. This is called the automatic mode of information processing. If a given stimulus is of a particular significance, the stimulus is further processed in the later stage of information processing. In such a situation, attention of the subject is attracted to the stimulus and part of the resource of attention is then allocated for the processing of the given stimulus (e.g., Kahneman, 1973; Öhman, 1979). This is called the controlled mode of information processing. The automatic mode is characterized by parallel, non-attention-limited processing of stimulus, whereas the controlled mode implies serial, attention-limited processing. This notion of automatic/controlled processing has been proposed by Schneider and Shiffrin (1977; Shiffrin & Schneider, 1977). Kahneman (1973) has suggested the resource of attention to be necessarily limited for capacity of information processing. The notion of limited processing capacity is often considered to largely overlap with conscious attention. This means that the allocation of the limited resource of attention for processing a given stimulus is consciously executed with subject's attention to the given stimulus. Therefore, when an OR is elicited in response to a given stimulus, the OR must be associated with the allocation of attentional resources (e.g., Kahneman, 1973; Öhman, 1979; Dawson, 1990;
Näätänen, 1990), namely, the controlled mode of information processing.

In conclusion, the examination of the nature of attention-related, significance properties of stimuli is likely to be important for interpreting the OR. Furthermore, the notion of the two types (i.e., automatic and controlled) of information processing may well be needed to fully explain the OR characteristics. It is therefore suggested that the relationships between the OR and EDA in human behavior can be interpreted in terms of information processing in the brain.

2.1.3.2 Emotions

In the research field of psychophysiology, EDA is often thought of as an index of human emotions, such as happiness, surprise, anger, fear, sadness, and disgust (e.g., Levenson, 1988; Boucsein, 1992). Recently, some researchers (e.g., Collet et al., 1997; Lipp et al., 1997; Lipp et al., 1998) have investigated whether or not a number of autonomic responses, such as skin resistance (SR), skin conductance (SC), skin potential (SP), HR, blood pressure, skin temperature (ST), skin blood flow (SBF), respiratory frequency (RF), and blink reflex, to emotional stimuli are emotion-specific. Collet et al. (1997) examined six types of indices (i.e., SR, SC, SP, SBF, ST, and RF) of the ANS in response to given stimuli characterized to induce the six emotions (i.e., happiness, surprise, anger, fear, sadness, and disgust). The SR, SC, and SP were categorized as electrodermal indices, the SBF and ST were as the thermovascular, and RF was as the respiratory. Using these ANS indices, Collet et al. compared the emotions to each other, thus comparing 15 pairs of emotions. For the electrodermal indices, a systematic decrease in SR was observed after stimulation, with an increase in SC. The duration of these changes in SR and SC differed for different emotion and therefore identified three groups of emotions: group 1 was of anger and happiness; group 2, fear; and group 3, surprise, sadness, and disgust. Furthermore, each type of emotion in 13 pairs was identified from one another by means of particular electrodermal indices. For example, the amplitude of SC differentiated the emotion of surprise from disgust. For the thermovascular and respiratory indices, 14 emotion-pairs were distinguished by two thermovascular, SBF and ST, and respiratory, RF, indices. However, changing patterns of the ANS indices in response to each emotion differed from each other. This indicates that the ANS responses are emotion-specific. Collectively, these results showed that all of 15 emotion-pairs were distinguished by electrodermal and thermovascular/respiratory indices. Collet et al. thus suggested that a specific response of each of the ANS indices was associated with each emotion. It is
therefore concluded that, in order to examine the human emotion, an electrodermal index should be used in a combined form of one or two ANS indices.

2.1.3.3 Voluntary movements

It has already been known that voluntary movements affect the elicitation of EDA. Siddle et al. (1979, see previous Section 2.1.3.1.3) found that when subjects had to press a button in response to a given stimulus, the SCR appeared to be larger than the SCR when any motor response was not required to do. The amplitude of SCRs appearing for subjects who pressed a button was twice as large as those appearing for the other subjects who did not press the button. This finding seems to suggest that the voluntary movement (e.g., button-pressing movement) may affect the SCRs.

Effects of voluntary movements on the EDA have been investigated by the utilization of reaction time (RT) tasks. RT is often used as an index to indicate the time interval from the onset of stimulus presentation to movement execution (see next Section 2.2). Freeman (1940) examined the relationship between skin conductance level (SCL) and speed of reaction (i.e., RT). The SCL indicates the 'state' or activation level of the sympathetic nervous system. He measured the RT of a single subject under various states of alertness, with the subject's alertness conditions ranging from half asleep to extremely tense. Freeman found an inverted U-shaped relation between SCL and RT, that is, RTs were fastest at moderate SCL and were slower at both high and low SCLs. Freeman's finding has often been referred to in support of the early activation concept that the relationship between the level of physiological activity and behavioral performance is of an inverted U function (e.g., Woodsworth & Schlosberg, 1954).

In addition, Surwillo and Quilter (1965) measured RTs and changes in skin potential (SP) of 132 healthy males, aged 22 to 85 years, in an hour-long vigilance situation. The subjects were required to monitor the movements of a clock pointer. The clock pointer moved in a discrete 3.6-degree step per second. In addition, the clock pointer was often manipulated to travel a 7.2-degree step per second. This deviant movement of the pointer was termed "double jump." The subjects were asked to press a key as quickly as possible whenever they recognized a double jump. In such a situation, the SP spontaneously fluctuated independently of the 3.6- and 7.2-degree step movements. Surwillo and Quilter termed the spontaneous fluctuation of SP the 'skin potential responses (SPRs)' and counted the number of SPRs appearing for an 18-sec period before the onset
of each double jump. The subjects who showed a large number of SPRs was termed “labiles” (2.27 times in average), and the other subjects who showed fewer SPRs was called “stabiles” (0.73 times in average), according to the terminology of Lacey and Lacey (1958). RTs for the labiles (488 msec) were significantly shorter than those for the stabiles (540 msec). This suggested that autonomic labiles (i.e., the subjects who showed a large number of SPRs) could respond faster than stabiles.

It is accordingly suggested that the production of voluntary movements may affect the elicitation of EDAs. EDAs have been generally categorized into two types in terms of situation at which the EDAs appear. One type of EDAs is immediately elicited in response to a specific stimulation and is termed phasic EDAs, such as SCR and SSR. The other type of EDAs is relatively stable and is termed tonic EDA, such as SCL. Freeman (1940) examined the tonic changes in SCL during various attentional states of subjects. As already described, Surwillo and Quilter (1965) examined the number of SPRs which occurred as a type of tonic EDAs during the time interval preceding the production of voluntary movements. These tonic EDAs, such as the SCL examined by Freeman and the SPRs examined by Surwillo and Quilter, were used to evaluate the preparatory state of subjects when they were asked to produce a motor response to a given stimulus. In such a task condition, a given stimulus is likely to be characterized in terms of ‘task relevance’, because the subjects are asked to perform/produce a voluntary movement in response to the stimulus. The task-relevant nature of a given stimulus has often been found to invoke a phasic EDA, such as SCR and SSR (Roth, 1983; Osada et al., 1998a, see Section 2.3.1). However, the effect of task-relevant stimuli on the appearance of phasic EDAs (e.g., SSR) has not yet been fully examined.

2.1.4 Sympathetic Skin Response (SSR)

Sympathetic skin response (SSR, Shahani et al., 1984), which is a type of the EDA, has been used in a clinical test of functions of a polysynaptic reflex. SSR is usually evoked by a startling stimulus. Such stimulation evokes afferent signals and these signals are delivered to the supra-spinal nervous system through diverse afferent pathways, and then to a common efferent pathway through the spinal cord, pre- and post-ganglionic sympathetic fibers, and sweat glands as effectors.

In general, patients with a neurological disease in the peripheral and central nervous system show abnormal waveforms of the SSR (see review, Arunodaya & Taly,
1995). For example, it has been shown (Watahiki, 1987b; Niakan & Harati, 1988; Zrur et al., 1993) that the SSR does not appear in patients with diabetic neuropathy. Yokota et al. (1993a) showed that fifty percent of 87 patients with varied types of cerebellar degeneration had abnormality of SSR. Hirashima et al. (1996) showed a high incidence of abnormal SSRs and small amplitudes of SSRs arising with the severe Parkinson's disease. Braune et al. (1997) also reported that SSR arose in 50 patients with Parkinson's disease with a long latency and small amplitude of the SSR, which were correlated with age, and that the longer the patient's history of the disease was, the more the abnormal SSR occurred. For patients with brain infarction SSR was reported to decrease in amplitude and prolong in latency (Korpelainen et al., 1993). These findings suggest that the elicitation of SSR may be influenced by the activation of the brain regions, such as the cerebellum, basal ganglia, hypothalamus, limbic structure (Section 2.1.2.2), and the cerebral cortex (Section 2.1.2.3), which are all important for the production of movements.

The amplitudes of SSR are likely to be degraded when the level of awareness or arousal of subjects becomes lower (Mimori & Tanaka, 1992). Awareness/arousal is thought to affect the attention-demanding, controlled mode of information processing, which may act an important role in cognitive functions of the brain. In voluntary movements, cognitive brain functions also mediate the stimulus evaluation and movement-related processes in the brain (see later Section 2.2.1). In this context, the SSR has been suggested to be mediated by the cognitive brain functions as well as sympathetic functions (e.g., Mimori & Tanaka, 1992; Arunodaya & Taly, 1995; Aihara et al., 1998; Osada et al., 1998b). The literature on cognitive brain functions subserving voluntary movements is examined in the following section.

2.2 INFORMATION PROCESSING IN THE SENSORY-MOTOR SYSTEM OF THE BRAIN

Cognitive functions of the human brain have often been examined using some indices, such as reaction time (RT), electroencephalogram (EEG), and event-related potentials (ERPs). These indices are thought to reflect processing of the environmental information (i.e., signal or stimulus) in the brain. Such information processing approach is a usual technique for clarifying the brain functions. In this section, previous studies on the RT and EEG in investigating the information processing in the brain with voluntary movements are first reviewed and the literature on the ERPs is then examined.
2.2.1 REACTION TIME (RT) AND ELECTROENCEPHALOGRAM (EEG)

Reaction time (RT) is often used as an index of the brain function. The RT reflects a total time spent for information processing during the interval from the onset of given stimulus to the production of motor response. The RT is shortened when a warning stimulus (WS) is presented to the subject before the presentation of imperative stimulus to which the subject is asked to respond (Teichner, 1954; Sanders, 1980). In addition, when a subject performs one motor response to one stimulus which is chosen from among various stimuli, the RT of the subject becomes later. This is called the choice RT, and the more choices, the later it (Hick, 1952; Hyman, 1953). In the research field of experimental psychology, a number of studies have been conducted on the RT as an index of cognitive information processing of the human brain. The methods used in such studies are to operate variables in psychological events corresponding to various stages of information processing, to investigate the time needed for these processing, and to assess temporal constructure and functions of whole information processing. These are called 'mental chronometry' (Kutas et al., 1977; McCarthy & Donchin, 1983; Tadai et al., 1986; Verleger, 1997).

The RT has often been examined using the electromyogram (EMG) and then separated into two components, EMG-RT (or premotor time, PMT) and motor time (MT). The EMG-RT shows the time interval from the onset of given stimulus to the onset of EMG bursts, the MT shows the time interval from the EMG onset to the production of motor response. It has been suggested that there is no correlation between the EMG-RT and MT in individual. This means that a prolongation of RT is mainly due to a prolongation of the EMG-RT. Studies on the RT have thus discussed on the neural mechanism controlling voluntary movements. For example, Broadbent (1971) have suggested that a shortening of RT (e.g., EMG-RT) under a situation where a warning signal (WS) existed, indicated a preparatory activation of the brain for the voluntary movement.

Since an electrical activity of the brain, that is, the electroencephalogram (EEG), was recorded in humans in 1929, the effect of the brain activity on the RT (or EMG-RT) has been examined. For example, Jasper and Penfield (1949) have shown that rhythmical activity of the EEG at the sensory-motor area of the brain disappeared preceding the production of voluntary movements. Surwillo (1969) has suggested that frequency component of the EEG has significant correlation with RT. In addition, Groves and Eason
(1969) investigated the effect of vigilance and attention on visually evoked EEG and the RT, suggesting that the RT shortened at suitable vigilance (or attention). Yingling (1980) suggested that the beta rhythm of the EEG in central area was related to voluntary movement, and reflected the primary planning and controls of voluntary movements in the brain. Pfurtscheller (1981) has shown that the beta rhythm of EEG decreased significantly during a voluntary movement of the hand. He called this phenomenon beta desynchronization. It has been also shown that such desynchronization occurred at the sensory-motor area of the brain during not only the voluntary movement of the hands but also that of the feet. In contrast, Nashmi et al. (1994) have shown that the beta rhythm of the EEG significantly increased at sensory-motor area during preparation periods of voluntary movements. According to these findings, it is agreed that the beta rhythm of EEG desynchronizes (or decreases) preceding and during movements but synchronizes (or increases) after movements (Salmelin & Hari, 1994a; Salmelin & Hari, 1994b; Stancák & Pfurtscheller, 1995; Pfurtscheller et al., 1996a; Pfurtscheller et al., 1996b; Stancák & Pfurtscheller, 1996a; Stancák & Pfurtscheller, 1996b; Stancák et al., 1997).

Although these findings on both RT and EEG, the two indices are suggested to be not able to examine various stages of information processing in the sensory-motor system of the brain. When one performs a voluntary movement in response to a given signal/stimulus, two types of information processing are thought to be executed in the sensory-motor system of the brain (Hiramatsu et al., 1985a; Tadai et al., 1986). One type of information processing includes stages of stimulus identification, decision making, and context updating. This is the stimulus (or stimulus evaluation) process. The other type of information processing includes response selection, response programming, and response execution. This is the behavior (or movement-related) process. Both the RT and EEG are not able to investigate the two types of information processing in the sensory-motor system of the human brain. Because, 1) the RT can not reflect actual activity of the brain, and 2) the EEG only reflect the state of the brain activities. In contrast to both the RT and EEG, the event-related potentials (ERPs) of the brain have been suggested to be able to evaluate the two types (i.e., stimulus evaluation and movement-related processes) of information processing in the brain.

2.2.2 EVENT-RELATED POTENTIALS (ERPs)

Electrical potentials of the brain elicited by a given signal (or stimulus) of the external environment are recorded from the scalp, and are divided into two types in terms
of their latencies. One type of the brain potentials is directly elicited by sensory, visual and auditory stimuli, showing short latency under about 100 msec. These are called the evoked potentials (EPs). Because the EPs are constantly elicited by external and physical stimuli, they are often called the 'exogenous potentials.' The other type of the brain potentials shows longer peak latency (more than about 100 msec) as compared with the EPs, being called the event-related potentials (ERPs). The ERPs are thought to be elicited with various stages of information-processing occurring in the brain, and are often called the 'endogenous potentials'.

The EPs/ERPs have often been recorded with combination of the techniques for non-invasive observation of the brain, such as PET, MRI, and single photon emission computed tomography (SPECT). Such studies have focused on elucidation for the generator of the EPs/ERPs, obtaining many important results (as shown in later Section 2.2.2.2.2). Furthermore, the ERPs are used to examine the physiological and/or psychological activities of the brain in information processing for the meaningful stimuli. For example, it has been suggested that an N140 component of ERPs which is evoked by somatosensory stimulus is sensitive to attentional state (i.e., awareness, consciousness, or arousal level) and that a P300 component reflects allocation of attentional (or processing) resources in the human brain. Furthermore, amplitude of the P300 is thought to be sensitive to meaning (or significance) of the eliciting stimulus. Such the attentional state, resource allocation, and stimulus meaning (significance) are suggested to have close relation with the elicitation of EDA (e.g., SSR). In the following part of this section, the literature on both N140 and P300 components of ERPs are therefore examined.

2.2.2.1 N140 component of somatosensory ERPs

The N140 component, a vertex negativity occurring with the somatosensory stimulation, has been much less investigated than that with the auditory stimulation (i.e., N1 or N100 component of auditory evoked potentials, for a review, see Näätänen & Picton, 1987). In general, the N140 (or N1 and N100) has been found when a subject is examined in the cognitive tasks. It has therefore been suggested that the N140 (N1 and N100) has relationship with the subject’s attention. Desmedt and his colleagues (Desmedt & Robertson, 1977; Desmedt & Tomberg, 1989) and Josiassen et al. (1982) have demonstrated that the amplitude of N140 was enhanced when a subject was asked to respond to a given (e.g., target) stimulus with a motor response. Furthermore, Desmedt and Robertson (1977) have shown that the amplitudes of N140 with nontarget stimulus
delivered to the same hand as the targets are larger than those with identical stimuli applied to the contralateral hand. In such situations, it is considered that the subjects pay their attention to the given stimuli. These findings therefore suggest that the N140 is sensitive to the subjects' attentional state. It has also been suggested that even a stimulus presented to one ear contralateral to the target ear may yield the auditory N1 waves that are enhanced relative to those of an ignore condition (Desmedt & Tomberg, 1989; García-Larrea et al., 1991). Thus, the somatosensory N140 component appears (i) to be larger and to possibly culminate later for stimuli that are attended than for those that are ignored and (ii) to reach maximal amplitude in response to target stimuli (García-Larrea et al., 1995). These characteristics of somatosensory N140 component are similar to those observed for the so-called processing negativity (PN, Näätänen et al., 1978) or negative-difference (Nd, Hansen & Hillyard, 1980), a cognitive component of evoked potentials described originally in the auditory modality. Both the PN and Nd are considered to index the concordance between a particular sensory stimulus and the one to which the subject is asked to attend. Therefore, it is concluded that the N140 component is sensitive to attention paid by subjects to given stimulus (Desmedt & Robertson, 1977; García-Larrea et al., 1995; Hatta et al., 1997).

Hatta et al. (1998) have shown that the N140 is affected by preparation for voluntary movement. They examined the N140 and other somatosensory evoked potentials (P40, N60, P100, and P200) in response to electric stimulations of the median nerve at the wrist prior to imperative stimuli during a reaction-time task in humans. The results showed that the amplitudes of all the potentials (except the P40) evoked by the electric stimulations were significantly increased throughout preparatory period for movement. Hatta et al. suggested that modulations of these potentials prior to movement onset stemmed from a cortical origin, which was activated involving a preparatory set for voluntary movements.

The neural generator of the N140 component has not yet been clarified. Desmedt and Tomberg (1989) suggested that the prefrontal areas (especially area 46) might play an important role for attentional processes. Hatta et al. (1997) showed that the somatosensory N140 was largest at frontal site (Fz) than other central and parietal sites, supporting the notion of Desmedt and Tomberg. Other researcher suggested another generators for the N140 component (e.g., the frontal cortex, Allison et al., 1992; the secondary somatosensory area, SII, Tarkka et al., 1996). Nakajima and Imamura (1996) investigated
neural generators of N140 using the dipole tracing method. They estimated that the generators located in areas of which from central to inferior areas of the lateral sensorimotor cortex. It still has been argued for the neural generator(s) of the somatosensory N140.

2.2.2.2 P300 components of ERPs

In contrast to the somatosensory N140, a P300 component of ERPs has been well investigated by many researchers. Sutton et al. (1965) discovered a late positive ERP wave evoked by a stimulus delivering significant information for the given task. Because the positive component had a latency of about 300 msec after presentation of the stimulus, it was called P300. In addition, the P300 often appears as the third positive deflection after the stimulus presentation, being called the P3.

The P300 is recorded from the scalp in the visual, auditory, and somatosensory stimulations. In contrast to the early component of the ERPs (e.g., N140 and N1), it has been shown that the scalp distribution of P300 reveals no substantial differences among the three modalities (i.e., visual, auditory, and somatosensory, Snyder et al., 1980).

It has been known that both the latency and amplitude of P300 reflect cognitive functions of the brain, such as stimulus processing time and allocation of attentional resources, in much more detail than the other indices, such as RT and EEG. Both the cognitive functions (i.e., stimulus evaluation and attentional allocation) of the brain are thought to be critical factors for the elicitation of EDA. Therefore, in the following parts of this section, the literature on the P300 is examined.

2.2.2.2.1 Subcomponents of P300

The P300 has usually recorded using a version of oddball paradigm. In the oddball paradigm, two stimuli, different in frequency, are often presented in a same modality: high frequency stimulus is ‘standard’ and low frequency stimulus is ‘target’. Frequent standard stimuli are presented in a high probability with a range of 80 to 90 percent, and infrequent target stimuli are in a low probability with a range of 10 to 20 percent. The P300 appears when the infrequent target stimulus is presented to the subjects. Such an infrequent target stimulus has a nature of rarity (i.e., novelty). Furthermore, the subjects are often required to make a response in response to the target stimuli in the oddball paradigm. For example, subjects are instructed to count the number of
presentation of target stimulus (i.e., count task), or press a button (reaction task), then the P300 arises in response to the target stimulus. Such a target stimulus is characterized in terms of task relevance.

Both the novelty and task relevance of infrequent target stimulus presented in the oddball paradigm are suggested to invoke two types of P300. Squires et al. (1975b) have suggested two types of P300, that is, the P3a and P3b. Squires et al. showed that the P3a was observed when a rare stimulus was presented in a task in which subjects were asked to ignore the rare stimulus during they read a book. The amplitude of P3a was largest at the frontal and central electrode sites and appeared in latency with a range from 220 to 280 msec. Courchesne et al. (1975) also reported that a P3a-like potential appeared when an infrequent stimulus was presented to subjects who were asked to ignore the infrequent stimulus. The P3a-like potential has often been called the novelty P3 (Knight, 1984; Yamaguchi & Knight, 1991b). In such a situation, it is considered that the subjects are forced to process unconsciously the rare stimulus while they are not required to pay attention to the stimulus. Such a forced attention of the subjects is referred as the passive-attention. Therefore, the rare stimulus is thought to be processed in non-attention-demanding, automatic mode of information processing in the brain (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977). The automatic mode of information processing is fast, non-attention-demanding, can occur in parallel with other simultaneous processing operations and is often unavoidable and cannot be consciously stopped or controlled (Imanaka et al., 1993). These features of the automatic processing mode are suggested to be corresponding with the processing of the OR-eliciting stimuli (Sokolov, 1963). That is, the OR appears automatically without any attentional resources, as well as the P3a and/or novelty P3.

In contrast to the P3a, it has been suggested that the P3b is observed when the subjects are asked to attend to a given stimulus. The P3b appeared in latency with a range from 310 to 380 msec, the amplitudes of P3b was largest at the parietal electrode site compared with the frontal and central sites. It has been suggested (e.g., Tueting & Sutton, 1976) that the P3b also appears when the subject is asked to respond to a given stimulus with a motor response. In such situation, the given stimulus (i.e., the target stimulus) is characterized in terms of task relevance, and the subjects must pay attention to the given stimulus. Therefore, the given stimulus is processed in the controlled mode of information processing in the brain (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977).
contrast to the automatic mode, the controlled mode of information processing is slow, attention-demanding, and serial in nature (Imanaka et al., 1993).

In the research field of psychophysiology, the brain regions where the electrical activities occur with such various events of information processing have been investigated using the techniques for non-invasive observation of the brain activity, such as the PET, MEG, and SPECT. These techniques have often been used with the recordings of ERPs and have provided the generator of ERPs, especially P300.

2.2.2.2.2 Generators of P300

There have been various findings on the neural generators of P300. Halgren et al. (1980) recorded the polarity-inverted P300 from implanted electrodes in hippocampal formation of epileptic patients. Okada et al. (1983) recorded P300 and P300-like magnetic field using MEG, estimating that the source of P300 existed in the hippocampus. These findings are interpreted to indicate that neural generators existing in the hippocampus may contribute to the surface-recorded P300. Subsequent studies (McCarthy et al., 1989; Picton, 1992; Knight, 1996) have supported the P300-hippocampal hypothesis of Halgren et al. and Okada et al. On the other hand, Yingling and Hosobuchi (1984) reported that a negative potential, corresponding to scalp-recorded P300, was recorded from implanted electrodes in the right somatosensory thalamus in patients with a history of chronically disabling pain stemming from back injury. Yingling and Hosobuchi thus suggested that P300 was generated in the thalamus or more dorsally located structures. Furthermore, Desmedt and Debecker (1979b; Desmedt & Debecker, 1979a; Desmedt, 1980) have proposed an alternate model for the generation of P300, in which P300 reflects transient inhibition of the reticulo-thalamo-cortical activating mechanisms, under control of the prefrontal cortex, following closure of the decision process in the target detection task. The major components of the activating mechanisms are the mesencephalic reticular formation, medial thalamus and prefrontal cortex. Since the activation of reticulo-thalamo-cortical mechanisms is associated with sustained negativity at the cortical surface, temporary relaxation may produce an apparent positivity at the scalp.

Yamaguchi and Knight (1991a) reported that association cortex in the temporal-parietal junction was critical for generating the scalp-recorded target P300 and novelty P3, whereas dorsolateral frontal cortex contributed preferentially to novelty P3 generation. Johnson (1988b) studied the bilateral distribution and overall amplitude of the P300 in
oddball paradigm in epileptic patients in whom the amygdala, hippocampal, and anterior
temporal lobe areas of the brain had been resected unilaterally. The results indicated that
there was no evidence of any left-right hemisphere asymmetry in the scalp distribution of
the P300 that varied as a function of the side of surgery in either the left or the right
temporal lobectomy patients. In addition, no statistically significant differences in overall
P300 amplitude or latency between the patients and healthy subjects were found. Johnson
thus suggested that the data did not support the P300-hippocampal hypothesis. Accordingly, findings from both intracranial and scalp recordings indicate that the neural
generators of P300 distribute in various region of the brain, not in single region
(Yamaguchi & Knight, 1991a; Nakajima et al., 1994; Hatta et al., 1997).

2.2.2.2.3 Correlates of P300 Latency

It has been suggested that latency of the P300 reflects the time spent for the
information processing of the given stimulus in the brain, as same as the RT. For example,
Kutas et al. (1977) and Duncan-Johnson and Kopell (1981) recorded both the P300 and
RT, suggesting that the latency of P300 reflected the time spent for the stimulus evaluation
process and that the RT was affected by the movement-related process. The stimulus
evaluation process includes a series of stages of encoding, identification, and
categorization of the given stimulus, while the movement-related process includes a series
of stages of the response selection and execution. That is, the two indices reflect different
functions of the brain.

It has often been shown that changes in the P300 latency caused with
manipulations of the experimental condition are inconsistent with those in the RT. A
disagreement of the correlation coefficients between the P300 latency and RT supported
these two processes. Kutas et al. (1977) recorded the RT and P300 evoked by a choice
stimulus to which the subjects were asked to categorize different words. In one condition,
the subjects were instructed to respond to the choice stimuli as fast as they possible (i.e.,
‘speed-maximizing’ condition), and in another condition as accurate as they possible
(‘accuracy-maximizing’ condition). The result showed that a correlation coefficient
between the P300 latency and RT was higher under the accuracy-maximizing condition
than under the speed-maximizing condition. Kutas et al. implied that under the accuracy-
maximizing condition the subjects responded to the stimuli after they completed evaluation
of the given stimuli, while under the speed-maximizing condition, the subjects initiated
motor response before they finished the evaluation of the given stimuli. Pfefferbaum et al.
Chapter 2 Review of Literature

(1983) also investigated the correlation between P300 latency and RT under speed-maximizing and accuracy-maximizing conditions using oddball paradigm. The subjects were asked to detect difference of length of line segments which were visually presented. They found that a correlation coefficient between P300 latencies and RTs was higher under speed-maximizing instruction than under accuracy-maximizing instruction. This is inconsistent with the results of Kutas et al. Pfefferbaum et al. implied that because the subjects’ task in their experiment (the subjects had to detect differences of length of line segment) was more difficult to the subjects compared with that used in the experiments of Kutas et al. (1977), the subjects responded to given stimuli after confirmation of the differences of the stimuli under accuracy-maximizing instruction, resulting the lower correlation coefficient. These results indicate that correlation of P300 latency and RT is influenced with the response strategy of subjects, “How I respond to the given stimulus?” Nishihira et al. (1999) found that both EMG-RT and P300 latency were increased after physical exercise, suggesting that the effects of physical exercise influenced the response selection stage of the movement-related process. Nishihira et al. (1999) have therefore supported the notion of Pfefferbaum et al. (1983), suggesting that the stimulus evaluation and movement-related processes are operated in parallel.

In addition to the stimulus (or stimulus evaluation) and behavior (or movement-related) processes, Baribeau-Braun et al. (1983) and Tadai et al. (1986) have thought that the organizing system controls both the two processes independent of them. Baribeau-Braun et al. (1983), in investigation using schizophrenics, suggested that late and inadequate information processing of schizophrenics was responsible for that they could not maintain stimulus and behavior processes using appropriate strategy. Hiramatsu et al. (1985a) expressed schematically a model for relationship between P300 and RT (p.1060). Hiramatsu et al. recorded ERPs with RT in patients with schizophrenia and normal subjects during a three-tone auditory discrimination paradigm. The subjects were asked to detect rare target stimulus with accurate and faster RT response, and to ignore both rare nontarget and standard stimuli. The result showed that RTs and P300 latencies evoked by rare target stimuli were nearly equal in both groups, however RTs in patients were delayed as compared with normal subjects. These results mean that the stimulus process (reflected by P300 latency) in the patients do not differ from that in the normal subjects. Hiramatsu et al. suggested that because the organizing system was impaired in the patients, the stimulus process could not transmit information to the behavior process, resulting delayed responses.
of the patients.

Collectively, it is considered that the P300 latency, at least, is affected by the strategy used for movement-related processes by the subjects in addition to reflecting the stimulus evaluation time.

2.2.2.4 Correlates of P300 Amplitude

It has been suggested that amplitude of the P300 is affected by the characteristic of a given stimulus. Johnson (1986; 1988a; 1993) has suggested that the characteristic of the stimulus which modulates the P300 amplitude is divided into three aspects: 1) subjective probability, 2) stimulus meaning, and 3) information transmission.

**Subjective probability:** The P300 amplitude is larger when the stimulus is more improbable. Duncan-Johnson and Donchin (1977) recorded ERPs as subjects listened to randomized sequences of two tones and counted one of them. They found that the amplitude of the P300 was inversely proportional to the probability of each tone. The P300 for the counted tones was slightly larger than that elicited by uncounted tones, but this effect was much smaller than the probability effect. This effect depends on the probability of the category in which a stimulus is perceived rather than the probability of the individual stimulus. Probability can be considered in terms of time - how often a particular stimulus occurs within a period - or in terms of stimuli - how many stimuli are of a particular kind. Fitzgerald and Picton (1981) suggested that the P300 was more closely related to “temporal probability” than to “stimulus probability (or sequential probability).”

Other effects of probability also play a role in determining the P300 amplitudes. Squires et al. (1976) maintained the global probability of a target stimulus over a block of stimuli but examined the responses to targets separately according to the exact sequence of preceding stimuli (the “local” probability). The P300 in response to the target stimulus was larger when the target followed a series of standard stimuli than it followed a series of other targets. Johnson (1986; 1988a) combined both global and local expectancies into improbability (subjective probability) aspect.

**Stimulus meaning:** The P300 generally occurs in response to task-relevant stimulus (Hillyard et al., 1973; c.f., Picton, 1992). The task-relevance nature of stimulus can be characterized as ‘stimulus meaning’. The stimulus meaning aspect is comprised of three variables: task complexity, stimulus complexity, and stimulus value.
The first, the complexity of task in which subjects are assigned to (e.g., counting or responding to given stimulus) is suggested to modulate the P300 amplitude. When the subjects are asked to count the presentation of the target stimulus (counting task), a P300 evoked with the target stimulus (e.g., Picton et al., 1971; Squires et al., 1973; Duncan-Johnson & Donchin, 1977; Johnson & Donchin, 1982). When the subjects are asked to respond to a given stimulus with a RT movement (reaction task), the amplitude of P300 evoked with the given stimulus becomes large as compared with that in the count condition (Johnson, 1986 #729, e.g., Tueting & Sutton, 1976). Furthermore, in addition to such counting and reaction tasks, when the subjects are asked to attend a feedback stimulus which indicate whether or not their performance are good (feedback task), the P300 amplitude is larger than those in the reaction task (Johnson, 1986). That is, the P300 amplitude increases from the counting task to the reaction task with a still larger P300 in the feedback task. Johnson (1988a) suggested that the extent to which a stimulus must be processed (he called it the “processing demands”) associated with these tasks would follow the same order as shown by P300 amplitude (e.g., P300 amplitudes increase in order, counting < reaction < feedback).

The second, effects of stimulus complexity can be quantified by using traditional measures of difficulty, such as choice reaction time. For example, Kutas et al. (1977) had subjects count the occurrences of male names in a set of stimuli containing a mixture of 20 different male and female names. Kutas et al. and other experimenters (Johnson & Kopell, 1980; Johnson et al., 1985) found that word stimuli elicited substantially larger P300 in amplitude with longer RTs than those reported previously for more simple visual stimuli at the same levels of probability (e.g., Squires et al., 1977). A finding of the Kutas et al. (1977) study is that the effects of stimulus complexity were independent and additive to the effects of task complexity. In addition, it is known that the P300 latency become longer when it is difficult subjects to discriminate two or more stimuli (e.g., Pfefferbaum et al., 1983). Goodin et al. (1983) has confirmed that the P300 latency increased with stimulus difficulty as previously reported (Ritter et al., 1972; Kutas et al., 1977; McCarthy & Donchin, 1981).

The third variables on the stimulus meaning, value (or significance) of stimuli, is independent of either task complexity or stimulus complexity since, for example, the monetary or emotional significance of events can be varied in all task and stimulus situations. When monetary payoffs have been manipulated, larger P300s were elicited by
high-value stimuli than by low-value stimuli (Tueting & Sutton, 1976; Johnston et al., 1987). These three variables of stimulus meaning (or signal value) should make an independent and additive contribution to P300 amplitude (Johnson, 1993).

**Information transmission:** The term information transmission, as used by Johnson, is defined as the proportion (i.e., it will have a value between 0 and 1) of stimulus information received by a person relative to the total amount of information originally contained in the stimulus. Ruchkin and Sutton (1978) originally proposed that P300 amplitude is modulated by the subject’s degree of equivocation. Equivocation, a term from classical information theory (Shannon & Weaver, 1963), means the amount of information loss that occurs during the presentation of a stimulus because of the subject’s posteriori uncertainty about having correctly perceived an event.

Johnson and Donchin (Johnson, 1978 #859; see Johnson, 1988a) found that P300 amplitude and task performance were linked to stimulus discriminability. In their experiment, the subjects estimated the passage of one second of time. After making each estimate, the subjects heard one of two tones that indicated whether their estimate was “correct” or “incorrect.” The two tones were therefore referred as feedback. The interval for correct estimates was manipulated so that the two feedback tones were presented with equal probability. Stimulus discriminability of the feedback tones was manipulated by varying the intensity difference between the two feedback tones. The results indicated that when the discrimination between the two feedback tones was easy, both P300 amplitude and task performance increased. This suggested that both P300 amplitude and task performance were positively correlated with discriminability. In a second experiment, the same stimuli were presented in an identical manner, while the subjects were instructed to count one of the tones. In contrast to the results of the first experiment, P300 amplitude and counting accuracy were constant across all levels of discriminability. The only difference between these two experiments was that the subjects had an alternate source of feedback information in the time estimation task. That is, the subjects could continue to make their estimations by supplementing the external feedback (provided by the tones) with internal feedback from having practiced the task. Johnson and Donchin therefore considered that the subjects increased their reliance on their internal feedback as their equivocation about the identity of the feedback stimulus increased.

In conclusion, it is suggested that 1) unexpected events elicit larger P300 than expected events, 2) the P300 amplitude increases with stimulus and task complexity and
with stimulus value, and 3) P300 amplitude is proportional to the extent to which the full amount of stimulus information is transmitted to the subject. For the subjective probability, the unexpected stimulus is thought to be characterized in terms of stimulus novelty. Such a novel stimulus is suggested to be processed in the automatic mode of information processing in the brain. For the stimulus meaning, when the subject are asked to respond to a given stimulus, the given stimulus is thought to be characterized in terms of task relevance. The task relevant stimulus is suggested to be processed in the controlled mode of information processing in the brain. The automatic processing is non-attention-demanding, while the controlled processing is attention-demanding (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977; Imanaka et al., 1993). Further, for the information transmission, the amount of stimulus information transmitted to the subject decreases when the subject is not attentive to the stimulus. These notions suggest that the P300 amplitude has relation with the resources of the subjects' attention which has the limited capacity (Kahneman, 1973, see the previous Section 2.1.3.1.5). In other words, the P300 amplitude reflects the amount of attentional resource allocated for the cognitive processing of a given stimulus (this is often called the cognitive capacity).

2.2.2.3 Significance of P300

It has been suggested that the P300 is associated with a variety of cognitive activities, for example, uncertainty resolution (Sutton et al., 1965), stimulus evaluation (Kutas et al., 1977), decision making (Johnson & Donchin, 1982), post-decision closure (Desmedt, 1980), and context updating (Donchin & Coles, 1988). Hillyard et al. (1971) and Squires et al. (1975a) have suggested that confidence in a decision regarding detection is related to P300 amplitude such that higher amplitudes were associated with greater degrees of confidence. Further Squires et al. (1973) used a signal detection task in which subjects were asked to decide whether a very low-level auditory signal was heard during a specified time interval. Squires et al. showed that an early component of the ERP (N1, peaking between 140 and 190 msec) and P300 (354 and 450 msec) represented aspects of decision making, suggesting a relationship between P300 amplitude and decision confidence. Donchin and Coles (1988) considered that P300 components evoked by target stimulus reflect context updating, which is subsequent memory storage processes that enable the subject to use current information to prepare for future events. Desmedt (1980) suggested that P300 reflect post-decision closure, which is a closure of cognitive processes relating both the actual decisions about the target stimulus and activation of the motor
response. All of these are compatible with the assumption that the P300 manifests an inhibitory event in neural system of the brain (Birbaumer & Elbert, 1988).

Cognitive capacity (or attentional resource) provides a central theoretical notion for the analysis of the P300. This notion implies an economical perspective on cognitive function of the brain, where different types of cognitive activities have to compete for cognitive capacity. It is, of course, an old notion that consciousness is selective in the sense that it can deal with only one thing at a time. To quote James' famous definition of attention: "It is the taking possession by the mind, in clear and vivid form, of one out of what seems several simultaneously possible objects or trains of thought...It implies withdrawal from some things in order to deal effectively with others" (p.403-404, James, 1890). A capacity view of this selectivity implies that the limitations are strategic rather than structural, that the resources can be flexibly allocated over activities depending on overall current plans and motivation.

On the basis of the previous studies, it is suggested that the amplitude of P300 represents processing capacity or attentional resource to be allocated in processing the given stimuli/events and that the latency of P300 reflected processing time spent in such cognitive processes.

2.2.2.4 Go- and NoGo-P300

Several investigators (Simson et al., 1977; Pfefferbaum et al., 1985; Gemba & Sasaki, 1989; Jodo & Kayama, 1992; Roberts et al., 1994) have reported, if a human subject is asked to respond to one class of stimuli (Go) and withhold the Go response to the other (NoGo) in a Go/NoGo paradigm, respective types of P300 component appear in response to each class of stimulus. Go/NoGo paradigm may be of ultimate clinical relevance because the inability to perform a delayed alteration task is a common feature of dementia and lesions of the frontal and limbic structures (e.g., cingulate motor cortex) of the brain, and one component of such a task is the withholding of a response (Pfefferbaum et al., 1985). In the Go/NoGo paradigm, a warning stimulus (WS) preceding either Go or NoGo stimulus is often presented. When Go stimuli are presented the subject have to execute the to-be-required motor response (the response is informed the subjects by WS), then the P3b-like positivity, Go-P300, appears. On the other, when NoGo stimuli are presented, the subjects have to withhold the to-be-required movement; a positive component appears with longer latency comparing with Go-P300. The positivity is called
NoGo-P300, which has central-maximum amplitude. From these findings, it is suggested that the NoGo-P300 reflects the suppression of prepared motor response (De Jong et al., 1990; Roberts et al., 1994), and that activation of right frontal regions are responsible for the inhibitory brain functions (i.e., NoGo-P300, Strik et al., 1998).

During the Go/NoGo paradigm, a negative potential (N2) is often elicited by NoGo stimuli at a latency of 200-300 msec (Gemba & Sasaki, 1989; Jodo & Kayama, 1992). The N2 is predominant in frontal areas of the human brain, and its amplitude increases specifically in the NoGo trial. Similarly, in the prefrontal cortex of the monkey a surface-negative, depth-positive field potential is recorded, especially in the NoGo trial, at latency of 100-150 msec (Sasaki & Gemba, 1986; Sasaki et al., 1989; Gemba & Sasaki, 1990). This potential is termed the ‘NoGo potential.’ In studies on neural sources for the N2 and NoGo potential, using magnetoencephalography (MEG), Sasaki et al. (1993) showed that during NoGo trial in Go/NoGo paradigm current dipoles localized in the dorsolateral parts of the frontal lobes (probably in the prefrontal-premotor areas). This suggests that the NoGo decision and subsequent inhibition of voluntary movements are of the functional features of the human frontal cortex.

The ability to inhibit prepared movements is an important control option that allows efficient reactions to sudden changes in the environment. Such changes may arise as an unexpected consequence of one’s own behavior, or they may be due to extraneous factors. In both cases, unexpected changes may render prepared movements inappropriate, in which case these movements will need to be inhibited.

In conclusion, it is suggested that the P300 component of ERPs manifests a closure of neural activities in the brain. The closure of neural activities is preceded by excitation of the brain regions corresponding to the processing for given stimulus/signal. If the amplitudes of P300 increases, cognitive capacities (attentional resources) used in the processing of the given stimulus/signal should also be large. If the latencies of P300 decrease, the time spent for processing the stimulus/signal should also be short.

It is also suggested that the two subcomponents of P300 (P3a/novelty P3 and P3b) reflect different mode of information processing in the brain. P3a/novelty P3 reflects non-attention-demanding, automatic mode, and may have relations with OR. In contrast, P3b reflects the attention-demanding, controlled mode, being affected by task-relevance nature of given stimulus/signal.
2.3 SYMPATHETIC SKIN RESPONSE AND P300: INTEGRATION BETWEEN THE SYMPATHETIC NERVOUS SYSTEM AND THE BRAIN

Changes in the cortical and autonomic responses to a given stimulus have often called the event-related responses (ERRs, Rockstroh & Elbert, 1990). Rockstroh and Elbert have considered that the ERR refers to the systematic variations in the time course of such variables of both cortical and autonomic activities when an event is perceived and/or anticipated by the subjects.

Since early studies with respect to both EEG and ERPs, measurements of these autonomic nerve activities (e.g., EDA and HR) have been used to eliminate possible autonomic effects. It enables plausible explanations for observed variance in both EEG and ERPs in terms of cortical cognitive functions of the brain. However, Papakostpoulos (1973) proposed that a broader psychophysiological context is needed for investigation of changes in the ERPs. In the field of psychology, it is known that the autonomic activities, such as HR, blood pressure, and EDA, fluctuate by various emotional stimuli, and the psychophysicologists have developed these activities’ potentialities as indices of human feelings, anxiety, motivation.

In the field of psychophysiology, with respect to the preponderance of either phasic or tonic parameters of the ANS, it has been focussed either on responses to distinct stimuli or on physiological parameters as indicators of changes for more general states of subjects (e.g., HR and contingent negative variation, CNV, see Appendix A). On the other hand, stimulus-specific and phasic responses in the ANS were investigated in terms of the OR (see Section 2.1). Much work has been devoted to P300 as OR to single stimuli associated with a task. For example, the sensitivity of the P300 to conditional probabilities and task relevance has been shown (e.g., Johnson & Donchin, 1982). However, there have been few attempts to relate cortical responses (e.g., P300) with autonomic responses (i.e., SCR). Lacey and Lacey (1978) measured cardiac responses (i.e., HR) and P300 in an "oddball" paradigm. While the P300 discriminated only between rare and frequent stimuli, heart rate deceleration turned out to be sensitive to expectation and subjective probability estimation, being more pronounced for rare stimuli and for stimuli immediately preceding frequent events. Lacey and Lacey suggested that sensorimotor events were able to differentially modify the duration of cardiac cycle and that rarity of stimuli (or events) were sufficient, but not necessary, to produce cardiac cycle effects. Some researchers
(Woestenburg et al., 1981; Roth, 1983; Woestenburg et al., 1983, see later) have also tried to clarify the relationship between the autonomic (EDA) and cortical responses (P300) in OR processes.

Collectively, results of previous studies show that both central and autonomic ERRs is sensitive to relatively complex stimulus conditions. From the pattern of correspondences or dissociation, Rockstroh and Elbert (1990) conclude that the understanding of ERRs is ultimately interwoven with the uncovering of central-autonomic interactions.

2.3.1 EDA AND P300 AS OR

Roth (1983) has drawn certain conclusions about covariation between the SCR and P300. Conditions under which single stimuli elicit either an SCR or a P300 exhibit the features of (1) surprise (i.e., the stimulus occurs unexpectedly or is omitted; e.g., stimulus probability); (2) task relevance or signal value (i.e., significance of stimulus; e.g., the stimulus requires motor responses or cognitive work), and (3) salience (i.e., the stimulus has outstanding qualities; e.g., stimulus intensity). It is natural to call salient stimuli surprising and to consider them as having intrinsic signal value and being innately task relevant to the survival of the organism. However, for scientific purpose, it is desirable to use different terms for factors that can be distinguished operationally, he has considered under the heading “Surprise,” only experiments that manipulated probabilities and expectations, and under “Task relevance,” only experiments that explicitly manipulated this variable.

In view of the important role assigned to the cerebral cortex in OR theories (Sokolov, 1963), direct evidences about electrical reactions of the brain have to be measured concurrently with the other indices of the autonomic activity (e.g., EDA). Although, since much work has been devoted to ERPs to single stimuli (e.g., P300) associated with a task, there have been few attempts to record EDA (such as SCR, SPR, and SSR), concurrently. Woestenburg et al. (1981; 1983) investigated the influence of information value of visual stimuli (difference in bits, see p.192, 1981 and p.229, 1983) on habituation of ERPs and SCRs with repeating the stimulus presentation under both non-task- and task-relevant conditions. The habituation of the P300 amplitude under the task-relevant condition was restricted to the fronto-central electrode site, and was delayed as compared to that under the non-task-relevant condition. Also, information effects were
noticed on these fronto-central sites, but not on both P300 at parietal site and the SCR, these did differ between the two conditions. Woestenburg et al. therefore suggested that only the fronto-central P300 waves might be part of the OR, and that the task relevance affected the parietal P300 and the information value affected the frontal P300 but not on the SCR.

2.3.2 SSR AND AUTOMATIC PROCESSING

In Woestenburg et al's studies, the fronto-central and parietal P300 waves may correspond to P3a and P3b, respectively. P3a, or novelty P3, is sensitive to the novelty (or surprise) nature of the given stimuli, and is suggested to reflect automatic processing for the given stimuli. According to the Sokolov's OR theory, automatic (involuntary) processing of the stimulus (information) is critical factor for eliciting the OR.

Miyakawa et al. (1992) examined SSR and ERPs evoked by electrical stimulation applied to the median nerve at the right elbow joint. The subjects were not required any tasks by experimenter. The results showed that a positive subcomponent of the ERPs (P200b, latency about 245 msec) appeared to be enhanced when SSR was present. They suggested that the P200b subcomponent, which most likely corresponds to P3a, reflects OR, being especially elicited when SSR is also evoked. Using an auditory oddball paradigm, Ito et al. (1996) reported various changes in the CNS and ANS, such as an increment of skin sympathetic nerve activity (SSNA, it was directly recorded using a new method, microneurography), a decrement of skin blood flow, and the appearance of SSR and P3a following target stimulus. Ito et al. concluded that the P3a was related to the mechanisms that generate SSNA. These studies indicate that elicitation of SSR has relation with neural activities in the brain for automatic mode of information processing.

Deguchi et al. (1996), using three types of stimulus presenting in a sequence, showed that both SSR and novelty P3, evoked by novel stimulus in which the subjects were instructed to ignore, were closely correlated. Deguchi et al. suggested that the SSR was one part of the OR and affected by the frontal lobe function of the brain. Knight (1996) showed that damage of the hippocampus (which is thought of as a possible generator of P300) impairs amplitudes of both P3a (novelty P300) and SSR. He therefore suggested that the hippocampal region was important for detection of the novelty nature of stimulus. Halgren and Marinkovic (1995) suggested that these potentials (P3a or novelty P3 and SSR) reflect both the central and peripheral neural functions of ORs to novel or

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sufficiently deviant stimuli.

Finally, it is believed that SSR arises when the given stimuli are presented in a low probability, that is, when the given stimuli are processed in the automatic mode (e.g., 1997; Lagopoulos et al., 1998). This may suggest that the SSR has no relation with attention of subjects. If anything, the SSR arises when the subjects’ attention is automatically directed to the rare stimuli.

2.3.3 SSR AND CONTROLLED PROCESSING

While the OR responses may be elicited by different stimulus situations (i.e., expectancy mismatch, target match, or sensory overload), the antecedent conditions are similar, namely, a call for the reallocation of attention or increased processing resources under “task relevance.” Under task-relevant conditions, the OR-eliciting stimuli should be processed in the controlled mode of information processing of the brain (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977). When the given stimulus is processed in the controlled mode, the P3b appears. Amplitude of P3b (degree of ERR in the CNS) is sensitive to meaning of the task relevant stimulus (Johnson, 1988a). In addition, degree of the ERRs in the ANS (e.g., EDA) is affected by the stimulus meaning/significance (Siddle et al., 1979). It is therefore also needed to examine whether the EDA (i.e., SSR) is influenced by such a controlled mode of information processing or not.

Deguchi et al. (1996) also showed that, in some participants, the target stimulus to which the subjects were asked to press a button evoked both SSR and P3b but these responses tended to habituate. Because the subjects should perform the required movement in response to the target stimulus, the target stimulus is thought of as task-relevant. P3b component evoked with such task-relevant stimulus should appear when the given stimulus is processed in the controlled mode of information processing. Therefore, the result of Deguchi et al. may indicate that SSR also arises when the given stimuli are processed in the controlled mode. Deguchi et al. suggested that the P3b for target stimulus consisted of the two subcomponents, ‘true’ P3b and novelty P3 (or P3a). Nevertheless, in their study, target stimuli were given to the index finger in intensity of 1.5 times of sensory threshold, and novel stimuli were given to median nerve at the wrist in 100 V intensity. In addition, probabilities of these two stimuli were 0.22 and 0.11, respectively. Thus, because the two types of stimulus (i.e., target and novel) differ in its intensity and probability to each other, it may be difficult to compare the two types of SSRs evoked by each stimulus.
However, it is not clear that whether SSR arises or not when the stimuli are processed in the controlled mode.

Despite the amendment made to the original Sokolovian model of OR (see Section 2.1.3.1.1), the theoretical emphasis is still very much focused on the physical characteristics of stimulus. Sokolov (1990) proposed a multidimensional model of stimulus parameters (with frequency, intensity, time and color), and claimed that the triggering factor of OR would be a change along one of these parameters. In 1995, in contrast, Barceló et al. (1995) showed that the skin conductance response as OR (Barceló et al. called it the SCOR) was related to task demands (i.e., task relevance) and controlled processing of the brain. Barceló et al. measured both SCOR and the EEG wave in a visual-discrimination task within a warning-stimulus paradigm. Both the physical complexity of stimulation and task relevance was manipulated within subjects. Neither the SCOR nor EEG power (i.e., reduction of alpha and theta power, Barceló et al. called it “EEGOR”) were reliably affected by the physical complexity of stimulation alone. However, high task relevance significantly increased the magnitude of EEGORs and SCORs. These results were consistent with a model of orienting as a continuous dimension of resource allocation to current task demands, rather than the earlier automatic processing. Barceló et al. suggested that future OR research should be more concerned with the elaboration of a taxonomy of tasks like the one proposed for the clarification of ERPs (Gaillard, 1988), rather than with the creation of a multidimensional model of stimulus parameters.

Recently, Osada and her colleagues (Aihara et al., 1998; Osada et al., 1998a) showed that the elicitation of SSR was affected by arousal level or awareness of subjects. Healthy subjects performed three tasks in which they were asked to ignore (C paradigm), to attend (A paradigm), and to respond by a button-pressing movement to all of the given stimuli (B paradigm). The left median nerve was electrically stimulated 10 times, and both ERPs and SSR were recorded. In the results, in the C paradigm, the amplitude of both SSRs and ERPs were highest with the first stimulus and decreased in an exponential manner as the number of stimuli in sequence increased. Whereas, in both active attention paradigms (i.e., A and B), SSRs and ERPs decreased in a linear manner. While a P3a appeared in the C paradigm, in both A and B paradigms, a positive potential appeared about 250 msec after the stimulation at the frontal region. The frontal positivity ‘P250’ (Hatakeyama et al., 1998a; Hatakeyama et al., 1998b) is suggested to consist of two attentive components (i.e., passive and active attention) distinct from selective attention,
and may be associated with maintaining awareness. In addition, Aihara et al. (1998) added a self-paced movement paradigm (S paradigm) to Osada et al.'s experiments. The results showed that the SSR remained enhanced during the latter half of the S paradigm. In the A, B, and S paradigms, the bereitschaftspotentials (BPs, Kornhuber & Deecke, 1965) and movement-related cortical potentials (MRCPs), which were slow negative shifts preceding both stimulus and EMG onset, were clearly present. BPs and MRCPs are suggested to reflect the subjective anticipation for the appearance of a next 'target' stimulus and programming of the to-be-required motor response (Garcia-Larrea et al., 1992; Starr et al., 1995). Osada et al. and Aihara et al. therefore suggested that continuous elicitation of SSR had relation with attention and preparatory set of subjects. They also suggested that the cingulate cortex might play some part in modulating the SSRs in motivational behavior context.

A subcomponent of P300, i.e., P3b is suggested to be associated with the controlled processing mode (Halgren & Marinkobic, 1995). When a person attends in given stimuli during task, the stimuli should be processed in the controlled mode of information processing. Osada and her colleagues (Aihara et al., 1998; Osada et al., 1998a) considered that their P250 had not a feature as same as that of P3b.

2.3.4 **DOES SSR HAVE THE RELATIONS WITH VOLUNTARY MOVEMENTS?**

The results of Osada et al. (1998a) may also indicate that the elicitation of SSR has relation with production of the voluntary movement. In the signal-triggering task (B paradigm) of Osada et al.'s experiment, subjects were asked to perform a voluntary movement. When one performs a voluntary movement in response to a given stimulus, the stimulus should be processed in the controlled mode of information processing in order to analyze their content or information. Moreover, the to-be-required movement has to be selected and the motor program for execution of the selected movements has to be provided. As previously mentioned (Section 2.2.2.1.3), information processing of the brain in analyzing the stimulus content/information consists of the stimulus evaluation and movement-related (behavior) processes (Baribeau-Braun et al., 1983; Hiramatsu et al., 1985a; Tadai et al., 1986). If activities of the SNS change during voluntary movements, it is likely that either the stimulus evaluation or movement-related processes relating to voluntary movements contribute to the sympathetic activities. For the stimulus evaluation processes, stages of stimulus identification, decision-making, and context updating are reflected in ERPs (e.g., N140 and P300). It enables examining the effectiveness of
subjects’ attention, task relevance, and stimulus meaning on sympathetic nerve responses (i.e., electrodermal responses such as SSR, SCR, and SPR).

For the movement-related processes, it is likely that each stage of the process (i.e., response selection, response programming, and response execution) affects the elicitation of SSR. Selection of response is made in conjunction with decision-making of the stimulus evaluation processes. For example, when subjects decide to perform a motor response, appropriate programs based on the subjects’ decision (i.e., motor program) are provided by the activities of the supplementary motor area (SMA). The SMA send the motor program to the primary motor area (MI), the MI then send the motor command to the to-be-activated skeletal muscles along with the motor program. Finally, the subjects perform required movements. Moreover, during the voluntary movement, motivation or intention of the subjects needs to occur concurrently. Motivation or intention of subjects is suggested to be produced by the activity of the anterior cingulate cortex (Devinski et al., 1995). In addition, subjects’ motivation or intention accompanies increment of attentional (or arousal) level of subjects. This is movement production process, which is produced by activity of movement-related areas of the brain (i.e., MI, SMA, and anterior cingulate cortex). The movement-related brain areas are suggested to affect the EDA (Sequeira & Roy, 1993; Devinski et al., 1995; Fredrikson et al., 1998), thus, the elicitation of SSR may also be influenced by the movement production process.

Recently, Fredrikson et al. (1998) investigated both cortical and subcortical areas of the brain important for controlling EDAs during visually stimulating conditions, using PET. They reported that EDA was positively related to regional cerebral blood flow (rCBF) in the left primary motor cortex (MI, area 4) and bilaterally in the anterior (areas 24 and 32) and posterior cingulate cortices (area 23). Negative relations were observed bilaterally in the secondary visual cortex (areas 18 and 19) and the right inferior parietal cortex (area 39), with a tendency also for the right insular cortex (areas 13, 15, and 16). Because these areas support anticipation, affect, and locomotion, they concluded that EDAs (e.g., SCR, SPR and SSR) seem to reflect cognitively or emotionally mediated motor preparation.

Devinski et al. (1995) suggested that the some parts of anterior cingulate cortex (termed affect division, including areas 14, 33 and rostral area 24) modulated autonomic activity and internal emotional responses. The other of anterior cingulate cortex (termed cognition division, including the caudal areas 24’ and 32’, the cingulate motor areas and
nociceptive cortex) was engaged in both response selection and attention-demanding information processing associated with skeletomotor activity. The affect division has connections with the amygdala and projects to autonomic centers of the brainstem, the cognitive division projects to the spinal cord and red nucleus of the basal ganglia (c.f., Devinski et al., 1995).

The motor program for voluntary movements enabling subjects to appropriately perform is provided by activation of the supplementary motor area (SMA). Then the primary motor area (MI) generates motor commands along with the motor program. The motor commands descend to skeletal muscles through the pyramidal tract, resulting in contraction of the skeletal muscles. Activations of the movement-related areas of the brain (i.e., SMA, MI, and anterior cingulate cortex) have been suggested to invoke the EDA, such as SCR, SPR, and SSR (e.g., Sequeira & Roy, 1993; Devinski et al., 1995; Sequeira et al., 1995; Fredrikson et al., 1998). It may therefore suggest that the SSR evoked with the stimuli (which require subjects to produce voluntary movements) may be controlled by the functions of movement-related brain areas (i.e., MI, SMA, and anterior cingulate cortex). That is, it is possible that the sympathetic nerve activity (e.g., SSR) is directly enhanced with occurrence of voluntary movements.

In contrast, when the subjects decide not to execute their motor response (NoGo decision), it is necessary to inhibit a production of the motor commands. Under such condition, it is suggested that both the NoGo-P300 and the N2 or NoGo potential should appear, reflecting the movement inhibition process (c.f., Section 2.2.2.3). The movement inhibition process is generated in the frontal brain regions, modifying the activities of the brainstem.

Schupp et al. (1994) recorded ERPs by means of presentations of five different letters (T, H, Z, O and X) for a fixed interstimulus interval (i.e., 2-sec). Subjects were instructed to perform voluntary movements (i.e., pressing a button) when an “X” appeared but only if an “O” preceded it. According to their differential meaning, the letter sequences were divided in three conditions: Go condition (O-X), NoGo condition (O-non-X), Irrelevant condition (a letter other than X was presented after a letter other than O). Furthermore, Schupp et al. recorded ‘eyeblink reflex’ (Brunia & Boelhouwer, 1988) using startle probe stimuli, which were presented 450 msec after presentation of a letter. The eyeblink reflex is a sensitive part of the startle response (like orienting response), reflecting excitability of the neuronal pools at the midbrain and brainstem (Brunia & Boelhouwer,
The results showed that under the NoGo condition a widespread P300-like positivity appeared with a central maximum in amplitude and the eyeblink reflex were inhibited compared with that under the Irrelevant condition. From these results, Schupp et al. suggested that the widespread P300-like positivity under the NoGo condition could be seen as a sign of the inhibition of movement production processes. Moreover, they supposed that such active inhibition of pre-programmed movements, provided by activation of the prefrontal cortex, was main reason for startle inhibition and P300-like positivity. The prefrontal cortex is suggested to control the autonomic nervous system (Neafsey, 1990), for example, elicitation of EDA may be affected by activation of prefrontal cortex (Raine & Lencz, 1993). It is therefore likely that the movement inhibition processes have relations with sympathetic nerve activities (e.g., elicitation of SSR).

In addition, irrespective of producing or inhibiting the voluntary movement, the motor program may affect the SSR. The motor programs are always variable. The human behavior changes appropriately coping to the given stimulus and/or situation, or sometimes coping to 'intention' of performer. Primates including human beings have higher brain functions relating to intention, motivation, and pleasure of creative and intellectual activities (i.e., voluntary movements) in addition to instincts and basic emotions of animals. Complicated voluntary movements are considered to be based on these functions. Therefore, the motor programs, which provided for the human behavior, should be arranged, affecting the SSR.

Collectively, it is worth to examine that whether the sympathetic nerve activity (i.e., SSR) enhance or not when one performs a voluntary movement. Because, activities of the SNS maintain the internal milieu (i.e., homeostasis of the human body) during voluntary movements, by means of the cooperation with the activities of parasympathetic and another systems (e.g., hormonal and myogenic). Barker and Saito (1981) found that the sympathetic nerve fibers innervated to both intra- and extrafusal muscle fibers (i.e., the muscle spindle and muscle fiber) as well as to blood vessels (i.e., arteries and arterioles). This suggests a possible contribution of sympathetic nerve activity to functions of skeletal muscle during voluntary movements.

The voluntary movements are essential elements of the human behavior. When the humans succeeds voluntary movements (i.e., physical activity), it is necessary that the optimum adaptation in cardiovascular, respiratory, nervous, and muscle systems (e.g.,
Vissing et al., 1991; Suzuki et al., 1997; Katayama et al., 1998). Given that such physical activities continue for a long time (i.e., long-term exercise), it is well known that the cardiovascular and respiratory systems undergo a transfiguration such as bradycardia, increasing the stroke volume, hypertrophy of the cardiac muscle, increasing the maximal oxygen uptake, increasing the vital capacity. For the muscle system, it is well known that hypertrophy of the skeletal muscles appears. These phenomena have been suggested to be adaptive, and have already been discussed in various research fields, including sport sciences and gerontology. Studies on effects of physical exercise (or physical fitness) on cognitive processes of human brain had been conducted (see a review, Tomporowski & Ellis, 1986), however, adaptive changes in the nervous system with physical exercise/fitness have not been clarified yet. Rather, this promising type of research has just been started: short-term exercise (e.g., Wiese et al., 1983; Petruzzello & Tate, 1997; Nishihira et al., 1999) and long-term exercise (e.g., Lardon & Polich, 1996; Polich & Lardon, 1997). For the details, see reviews on effects of physical exercise (or physical fitness) on information processing of the brain (Bashore, 1989; Polich & Kok, 1995, p.120-121).
CHAPTER 3 ISSUES TO BE INVESTIGATED, PARAMETERS, AND METHODS IN THIS STUDY

3.1 AIMS, ISSUES AND RATIONALES IN THIS STUDY

The main purpose of this study was to examine whether the sympathetic nerve activity is related to the preparation and production of voluntary movements. For this purpose, the following four experiments were conducted.

3.1.1 EXPERIMENT 1

SSR has been used in a clinical test to examine the functions of polysynaptic reflexes. SSR is usually evoked by a startling stimulus. Such stimulation evokes afferent signals and these signals are delivered to the supra-spinal nervous system through diverse afferent nerves, to the CNS to be processed, and then to a common efferent pathway through the spinal cord, pre- and post-ganglionic sympathetic fibers, and sweat glands as the relevant effectors. In general, patients with neurological disease in the central nervous system show abnormal features in their SSR waveforms. It also appears that the amplitudes of SSR are degraded when the levels of awareness of subjects become lower (Mimori & Tanaka, 1992). These facts suggest that the SSR could be mediated by cognitive functions of the higher centers of the brain as well as by sympathetic functions (Mimori & Tanaka, 1992; Arunodaya & Taly, 1995). However, the issue of the cognitive-sympathetic neuro-functional relationships has not yet been closely examined. It is therefore worthwhile to investigate the relationships between the sympathetic, particularly autonomic, nerve activity and the cognitive brain functions.

In investigating such an issue as described above, Miyakawa et al. (1992) examined a positive potential component, the P300, of ERPs in conjunction with SSR. The P300 is a well-known component of the ERPs which reflects a type of cognitive brain function, such as stimulus detection/evaluation. Cognitive functions of SSR can thereby be examined by making a comparison of ERPs, such as P300. The P300 component of ERPs is usually recorded using an oddball paradigm. A typical oddball paradigm consists of two types of stimuli (i.e., the target and standard stimuli) which differ in the probability of their presentation. In the oddball paradigm, the target stimuli, which subjects are required to
detect, are presented at a low probability (e.g., 20% of all stimuli presented in an experimental session, thus called ‘rare target stimuli’), and the standard stimuli, which the subjects are asked to ignore, at a high probability (e.g., 80%). Under such conditions, the P300 components clearly arise in response to the rare target stimuli but not to the standard. This implies that either the novelty nature of the rare target stimuli (mediated by the low probability) or task relevance (the target stimulus requires subjects to respond to it) or both may be responsible for evoking P300 components.

Squires et al. (1975b) suggested that the P300 components evoked by rare stimuli have two subcomponents, that is, P3a and P3b. The P3a could often be observed when a sufficiently rare stimulus (e.g., a loud, infrequent tone) is presented in such a task that subjects are asked to ignore the rare stimulus during reading of a book. Another type of P300 called "novelty P3" is also elicited when an additional, different type of rare stimulus (i.e., novel stimulus) is presented among both the usual rare and standard stimuli used in a type of oddball paradigm (Knight, 1984). Both the P3a and novelty P3 arise with relatively shorter peak latencies as compared with the latency of P3b. Sokolov (1963) suggested that such rare stimuli could automatically attract the subjects' attention to the stimuli per se even when the subjects concentrate their attention on other events or stimuli. Therefore, P3a and/or novelty P3 seem to relate to the automatic mode of information processing (Knight, 1996; Knight & Scabini, 1998; Lagopoulos et al., 1998). In contrast, P3b, of which the peak latencies appear at 60 to 80 msec later than the P3a and novelty P3, is usually evoked when the rare target stimuli (embedded among the frequent standard stimuli) require the subjects to either detect/count each target stimulus or respond to it with a voluntary movement (Picton, 1992; Knight & Scabini, 1998). The P3b is thereby suggested to be associated with the controlled processing mode (Halgren & Marinkobic, 1995).

The notion of automatic and controlled processing can originate with Schneider and Shiffrin (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977). Automatic processing is fast, non-attention-demanding, and can occur in parallel with other simultaneous processing operations, whereas controlled processing is slow, attention-demanding, serial in nature. According to this notion, the P3a and P3b are considered to be caused by different natures of stimulus; the novelty of the stimulus (relating to automatic processing) and the task relevance (relating to controlled processing), respectively.
Roth (1983) has shown that both the nature of stimulus novelty and task relevance can evoke the P300 and SCR (an EDA response). A number of studies have also shown that the SSR (another type of EDA response) is often observed accompanying either P3a (e.g., Miyakawa et al., 1992) or novelty P3 (Deguchi et al., 1996; Knight, 1996). These studies suggest that the stimulus novelty is at least an essential factor for evoking SSR. In contrast, Osada and her colleagues (Aihara et al., 1998; Osada et al., 1998a) have examined, from a slightly different point of view, both the SSR and P300 in two different tasks: 1) a reaction time task, in which subjects are asked to respond to target stimuli as quickly as possible by pressing a button, and 2) a self-paced voluntary movement task, in which subjects are asked to press a button voluntarily without any stimulus presentation. Osada and her colleagues have shown that both the SSR and P300 appear in the two tasks, therefore suggesting that SSR is evoked by the higher brain functions responsible for task-relevant processes (i.e., conscious target detection and motor production) rather than automatic detection of stimulus (i.e., stimulus novelty). In the oddball paradigm commonly used in studies of P300, subjects are usually asked to detect rare target stimuli and, in some studies, they are also required to respond to the rare target stimuli as quickly as possible with voluntary movements (e.g., pressing a button). The respective roles of the stimulus novelty and the task relevance in elicitation of the SSR during tasks requiring voluntary movements have not yet been examined. Therefore, it is worthwhile to examine this issue.

In Experiment 1, the effectiveness of the two types of stimulus nature, that is, the stimulus novelty and the task relevance, on elicitation of SSR were examined, using two different types of rare stimuli. The two types of rare stimulus are both characterized with stimulus novelty because of rare presentations, whereas they differed in the nature of task-relevance. One type of rare stimulus was presented to subjects as the target, to which the subjects were asked to respond by an elbow-extension movement, while the other was as the nontarget, which the subjects were asked to ignore. The frequent standard stimulus, which was supposed to be ignored by the subjects, was also presented. In such a three-stimulus oddball paradigm, some researchers (Pfefferbaum et al., 1984; Hiramatsu et al., 1985a; Hiramatsu et al., 1986) have shown that the rare target and rare nontarget stimuli elicited respectively two different P300 components, namely, target-P300 and nontarget-P300. It has also been suggested that the amplitude of the target-P300 (distributed over parietal sites) is generally larger than that of the nontarget-P300 (predominant at centro-
parietal sites), and that the latency of the nontarget-P300 is somehow longer than that of the target-P300. Such differences in amplitude, scalp topography, and latency between the target- and nontarget-P300 indicate that the specific nature of information processing must be different between the target and nontarget rare stimuli (Katayama & Polich, 1996b; Katayama & Polich, 1996a; Katayama & Polich, 1998). Hiramatsu et al. (1985a; Hiramatsu et al., 1986) and Pfefferbaum et al. (1984) conducted experiments using the three-stimulus oddball paradigm, and suggested that the effects of the stimulus novelty and the task relevance on the features of P300 can be evaluated separately by making a comparison between the two types of P300 (i.e., target- and nontarget-P300). Accordingly, the effects of stimulus novelty and task relevance (which were evaluated with the target- and nontarget-P300) on elicitation of SSR were thus examined in Experiment 1 using the three-stimulus oddball paradigm. Both P300 and SSR are believed to be mediated, in part, by the subjects’ attention. The N140 component is sensitive to subjects’ attention to given stimuli (Desmedt & Robertson, 1977; Garcia-Larrea et al., 1995; Hata et al., 1997, see Section 2.2.2.1). Therefore, to assess the attentional allocation of the subjects for the two types of rare stimuli, the N140 component of ERPs was also examined in Experiment 1.

3.1.2 EXPERIMENT 2

SSR may arise when a target signal (stimulus) is processed in the controlled mode rather than in the automatic. In this condition, the P3b component of ERPs are also evoked. The controlled mode of information processing is primarily activated in the processing of task-relevant stimuli, such as the stimuli which require subjects to either consciously detect each target stimulus from other nontarget stimuli or respond to them by the production of movements. Although both conscious target detection and movement production are well known to contribute to evoking P3b, it is still unclear which (i.e., target detection or movement production) is much more effective to evoke SSR.

For evoking P3b, conscious target detection is often used to require subjects to allocate their all attentional resources to the given stimuli. For example, when subjects are asked to count in mind the number of target stimuli which are rarely presented in the sequence of a large number of nontarget (standard) stimuli (counting task situation), the subjects attempt to be attentive to detect each target stimulus in the stimulus sequence. Such an effect of target stimuli on the subjects’ attention is termed the ‘target effect’ (e.g., Picton et al., 1971; Duncan-Johnson & Donchin, 1977; Johnson & Donchin, 1982). The
target effect occurs not only in counting tasks but also in reaction time (RT) tasks. For example, Tueting and Sutton (1976) showed that the typical P3b appeared when subjects were required to make a motor response to 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 (Johnson, 1986; Barrett et al., 1987; Johnson, 1988a). Both Barrett et al. (1987) and Johnson (1986) showed that the P3b amplitudes for 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 (1983) suggested that the 'signal value', or signal meaning, 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 (1986; Johnson, 1988a; Johnson, 1993) also suggested that the stimulus meaning is one of the factors determining the P3b amplitude (see Section 2.2.2.2.4). The term 'signal value' (Roth, 1983) is considered to be identical to the term 'stimulus value' originated by Johnson (1986), who proposed the stimulus value as one of the variables indicating/measuring the degree of stimulus meaning. According to this notion, it is suggested that when subjects are required to make a motor response to the target stimuli under a RT task, the requirement of motor response may probably provide the target stimuli with a stimulus meaning specific to motor production. This stimulus meaning specific to movement production should differ from the stimulus meaning under counting tasks.

Regarding the SSR in the context of motor response, it has been shown that the EDA responses are also enhanced when subjects are required to make a motor response. Bernstein and Taylor (1979) showed that SCRs (a type of EDA response) 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. (1979) 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. (1998a) have recently shown that SSR appears with both the bereitschaftspotential (BP,
Kornhuber & Deecke, 1965) and event-related desynchronization (ERD) of the EEG (Pfurtscheller & Aranibar, 1977) 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. 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 Experiment 2, the significance of both conscious target-detection and motor response on elicitation of SSR was discussed to elucidate the contribution of movement-related brain functions to the sympathetic nerve activity. To examine the effects of motor responses to the target stimuli on elicitation of SSR, an oddball paradigm was used under two conditions. 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. However, 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.

3.1.3 EXPERIMENT 3

In producing a voluntary movement in response to a stimulus, the information processing for this event involves at least two systems: the stimulus evaluation (i.e., stimulus identification, decision-making, and context updating) and movement-related systems (i.e., response selection, response programming, and response execution, c.f., Hiramatsu et al., 1985a; Tadai et al., 1986).

Issues of both the stimulus evaluation and movement-related systems have often been investigated using reaction time (RT) tasks. RT is the time elapsing from the onset of stimulus to the onset of actual movement, consisting of EMG-RT and motor time (MT). EMG-RT is the time from the stimulus onset to the onset of EMG burst, indicating the total time spent for information processing of stimulus identification, response selection and programming, and the delivery of motor commands to the muscles to be activated. MT is
the time from the EMG onset to the movement onset. Various experimental manipulations affect mainly EMG-RT but not MT. It is therefore suggested that changes in EMG-RT correspond to those in RT. A large number of psychological studies (e.g., Hyman, 1953; Sanders, 1980) have investigated the characteristics of RT and/or EMG-RT under various conditions. For example, it is well known that RT shortens in a reaction task in which a warning signal/stimulus, WS, is given to subjects prior to the appearance of imperative signal/stimulus, IS (this is called WS-IS paradigm, Teichner, 1954). This is because the subjects can anticipate the forthcoming presentation of IS and make a preparation for the desired motor response, resulting in quick processing of afferent inputs from the IS and fast execution of the motor response. Subjects' anticipation caused by the presentation of WS may direct and concentrate the subjects' attention to the forthcoming IS. The presentation of WS may also accelerate the response-related preparatory processes, such as the programming of motor commands for voluntary movements (i.e., motor program) before the presentation of IS.

The P300 component of ERPs has often been used as a means to examine the cognitive information processing of the given stimuli. In particular, the latency of P300 is thought of as a useful indicator to see the processing-time spent for stimulus evaluation. If the processing-time for stimulus evaluation decreases in a WS-IS paradigm, the P300 latencies should be shortened.

The relationships between the autonomic and cortical responses taking place during the WS-IS interval have been investigated by a number of researchers (see Appendix A, Lacey & Lacey, 1970; Gatchel & Lang, 1973; Yamazaki, 1977; Lacey & Lacey, 1978; Bohlin & Kjellberg, 1979; Simons et al., 1979; Lacey & Lacey, 1980; Simons, 1988; Wölk et al., 1989; Otten et al., 1995; Koers et al., 1997). For example, Saito and Mano (1992) reported that when a WS was presented, the skin sympathetic nerve activity was enhanced prior to the execution of voluntary movements (subjects were instructed to initiate the desired movements), suggesting that the cortical excitation arising in the preparation of voluntary movements also activates the ascending reticular activating system (ARAS). The excitation of ARAS, in turn, facilitates sympathetic nerve activity (Lindsley, 1960). Therefore, the cortical excitation should eventually facilitate, through the ARAS, the sympathetic nerve activity. However, it is still unclear whether the SSR (reflecting the sympathetic nerve activity) evoked by IS is changed or not when the IS requires subjects to produce a voluntary movement. If the sympathetic nerve activity is
facilitated by the WS (because of the cortical excitation for stimulus anticipation and motor preparation) as reported by Saito and Mano (1992), the SSR evoked by IS should also be affected by the presentation of WS. This was examined in Experiment 3.

In Experiment 3, the stimulus evaluation for the given stimuli (i.e., target stimuli) was manipulated by either the presentation (WS-IS paradigm) or withdrawal (oddball paradigm) of the WS. In both paradigms, subjects were asked to respond by extending the elbow to each target stimulus, presented at an appearance rate of 20% of all stimuli. The target stimuli in both paradigms should therefore be processed in a movement-related, controlled mode in both paradigms (Experiment 1 and 2). However, in the WS-IS paradigm alone, the target stimuli may be processed with relatively high anticipation and early motor preparation because of the presentation of WS. To examine likely differences in the nature of information-processing due to the presentation of WS, both the P300 latencies and EMG-RTs for target stimuli were compared between the oddball and WS-IS paradigms. In addition to the P300 and EMG-RT measurements, both the SSR for the target stimuli and the R-R intervals of electrocardiogram before the target stimuli were measured to examine possible changes in the sympathetic nerve activity, (e.g., Wölk et al., 1989; Otten et al., 1995).

3.1.4 EXPERIMENT 4

Movement-related processes (i.e., response selection, response programming, and response execution) should be mediated by the activation of brain areas responsible for motor production (e.g., the primary motor area, MI, supplementary motor area, SMA, cingulate cortex). In the WS-IS condition after the presentation of WS, a motor program for the required movement should be made by the activation of SMA as well as other areas of the brain (i.e., response selection and motor programming). Then, when the IS is presented as the imperative ‘target’ or ‘Go,’ the subjects make a decision to move and the MI is in turn activated. This results in the contraction of the relevant skeletal muscles (i.e., response execution).

However, if the second stimulus is ‘non-target’ or ‘NoGo,’ the subjects should decide to avoid the execution of the desired movement and make efforts to suppress the prepared motor program. This enables the subjects to stop the to-be-required (i.e., ‘pre-programmed’) movements. This is the motor inhibition process. Both the motor production and motor inhibition processes have recently been investigated by recording...
ERPs under the Go/NoGo paradigm (e.g., Simson et al., 1977, see Section 2.2.2.4, for the details; Pfefferbaum et al., 1984; Jodo & Inoue, 1990; Roberts et al., 1994). In the Go/NoGo paradigm, subjects were asked to perform a motor response when they perceived the ‘Go’ stimuli and avoid response when they perceived the ‘NoGo’ stimuli. It has been shown that the P300 component (similar to the P3b) appears when subjects respond to the Go stimuli (Go-P300), and that a slightly different type of P300 component appears when the subjects successfully avoid responding to the NoGo stimuli (NoGo-P300). The latter is characterized with both fronto-centrally-maximum amplitudes and longer latencies compared with those of the Go-P300. Pfefferbaum et al. (1984; Pfefferbaum et al., 1985) have confirmed that the topographic difference between the Go- and NoGo-P300 appears regardless of whether subjects perform a button press or simply count the number of Go stimuli. This suggests that the NoGo-P300 may relate to the motor inhibition process, which is functionally different from the motor production process.

In the Go/NoGo paradigm, it has also been shown that a negative potential (Simson et al., 1977; Pfefferbaum et al., 1985; Sasaki & Gemba, 1986; ‘N2’ in humans, Gemba & Sasaki, 1989; Sasaki et al., 1989; ‘NoGo potential’ in monkeys, Gemba & Sasaki, 1990; Jodo & Kayama, 1992) is elicited by the NoGo stimuli (see Section 2.2.2.4, for the details). In humans, Sasaki et al. (1993), using magneto-encephalography (MEG), have shown that during NoGo trials in the Go/NoGo paradigm, the current dipoles are estimated to localize in the dorsolateral parts of the frontal lobes. This suggests that the NoGo decision and subsequent avoidance of the execution of desired movements may be functionally mediated by the human frontal cortex. Therefore, the N2 component in humans may well reflect some aspect of the neural activity responsible for ‘response inhibition’ (Jodo & Kayama, 1992).

Schupp et al. (1994, for the details, see Section 2.3.4) suggested that P300 components evoked by the NoGo stimuli reflect a state of cortical disfacilitation suppressing the autonomic startle reflex. Schupp et al. recorded both ERPs by presenting different letters and eyeblink reflexes by presenting a startling probe stimulus after the letter presentation. The occurrence of the eyeblink reflex reflects the changes in excitability at the midbrain and brainstem, which is the origin of the autonomic activity. In their experiments, the subjects were required to press a button when they received a ‘Go’ letter, whereas they were asked to avoid the button-pressing when they received either ‘NoGo’ or ‘Irrelevant’ letters. The results showed that for the NoGo letters a widespread
P300-like positivity appeared with a maximum amplitude at the central (Cz) and the occurrence of the eyeblink reflex diminished, as compared with those for the Irrelevant letters. Schupp et al. suggested that the widespread P300-like positivity for the NoGo letters could be indicative of inhibition in the response processes (perhaps mediated by the activation of prefrontal cortex) and that such 'active inhibition of a pre-programmed response' was the main reason for both the inhibition of eyeblink reflexes and the appearance of widespread P300-like positivity. Cechetto and Saper (1990) have suggested that the prefrontal cortex predominantly influences the autonomic responses. It is therefore likely that the autonomic responses (such as the SSR) are also affected by the motor inhibition processes which avoid the execution of the required movements. This is examined in Experiment 4.

There were two experimental conditions in Experiment 4. In one condition, subjects were asked to respond to the Go stimuli by an elbow extension with approximately 20% of the maximal voluntary contraction (MVC). This was the MVC20 condition. In the other condition, the subjects responded to the Go stimuli at 40% of MVC (MVC40 condition). These conditions differed to each other in the muscular force of the movements. Therefore, the motor programs should differ between the two force conditions. Whether such a difference in the nature of motor programs affects the SSR was also examined in Experiment 4.

3.2 PARAMETERS

In this study, ERPs and SSR were used as indices of sensory-motor information processing in the CNS and the sympathetic nerve activity in the ANS, respectively.

Regarding the ERPs, P300 components of the ERPs were used as valuable indices indicating the higher brain functions in sensory-motor information processing for uncertainty resolution (Sutton et al., 1965), stimulus evaluation (Kutas et al., 1977), post-decision closure (Desmedt, 1980), and context updating (Donchin, 1981; Donchin & Coles, 1988).

The N140 component of ERPs was also used in the present study. The N140 component of ERPs is unique in somatosensory stimulation, and is considered to reflect the attentional condition, such as consciousness, awareness, and arousal level (Desmedt & Robertson, 1977). Desmedt and Robertson (1977) have reported that the amplitudes of
N140 were enhanced when a target or nontarget stimulus was applied for adjacent fingers in conditions in which the subject was forced to attend to the given stimulus. They suggested that the enhanced N140 amplitude indicated direct physiological evidence that the subject used a cognitive, effortful strategy in the earlier stages of cerebral neural processing.

The SSR is a type of electrodermal activity (EDA), which has been investigated by many psychophysiological researchers, although the skin conductance (SC) of EDA has more frequently been used. The SC is measured in terms of an electric device with either a constant voltage or constant current. In contrast, the SSR can easily be measured as the change in electric potential, like electroencephalography and electromyography. Due to this advantage, SSR has recently been widely used as an index of sympathetic nerve activity of the ANS in the research fields of neurology, clinical medicine, and clinical psychiatry. The SSR is also attracting some psychophysicologists’ attention.

In all of the experiments conducted in this study, subjects were asked to perform elbow extensions as the motor response to given stimuli. This type of motor response was used to investigate the relationships between voluntary movement, ERPs, and SSRs. Subjects were able to perform this type of movement accurately and quickly without any artifacts on EEG. Electromyogram (EMG) was also recorded from the agonistic muscles (the triceps muscles), and reaction times were measured as the duration from the onset of a given stimulus to the onset of EMG. The onset of EMG was determined as a sharp increase of EMG bursts. The reaction time (EMG-RT) was used as the response performance of the subjects.

### 3.3 METHODS AND DATA ANALYSES

#### 3.3.1 SUBJECTS AND APPARATUS

Neurologically normal volunteers participated in the experiments of this study. Informed consent was obtained from each participant. Subjects were comfortably seated in an armchair. A pile of two rectangular stainless-steel plates (20 cm long, 10 cm wide and 0.3 cm thick) was fixed on one side (the side of subjects’ preferred arm) of the 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 preferred forearm on the upper plate. Subjects contracted the triceps and/or the biceps muscles of
the upper arm, and the force was detected by the strain gauge. This was seen on the monitor window of an oscilloscope (VC-6723, Hitachi Co. Ltd., Japan). The oscilloscope was placed one meter in front of the subjects. The subjects were instructed to keep their eyes open and maintain a stable arousal level of consciousness during the experimental trials.

### 3.3.2 Stimulation

In the experiments of this study, somatosensory electrical stimulation was applied to the fingers. This type of stimulation affects all sensory receptors in the skin (pressure, touch, temperature, and pain), and afferent inputs derived from the stimulation are transferred to the CNS by sensory neuron innervating the skin. Pathways for somatosensory information from the sensory receptors to the CNS are known in details, and better understood than those of auditory and visual information. In a number of studies on ERPs, somatosensory stimulation has often been used to stimulate mixed nerves such as the median nerve. Such a stimulation can activate motor nerves as well as sensory nerves. If the stimulation is relatively strong, involuntary movements could appear as a reflex. As this study aimed to investigate the information processing during voluntary movements, somatosensory stimulation was applied to the fingers but not the mixed nerves.

Pain-related potential (Kakigi et al., 1989) is also likely to be mixed with ERPs. The intensity of stimulus was selected to range from two to three times the subjective sensory threshold measured at each finger, resulting in an intensity strong enough to be perceived accurately without pain.

Electrical square stimuli of 0.2 msec duration were generated by the electrical stimulators (3F46, NEC Medical Systems Co. Ltd., Japan). These stimuli were delivered to the fingers of preferred hand through ring electrodes attached at the middle of the first (cathode) and second phalanx (anode) of each finger. In Experiments 3 and 4, an auditory click (50-60 dB, 1 msec duration), delivered to the subjects via headphones, was used as a warning signal (WS). The auditory signal was generated using auditory stimulators (ST-5, Medelec, UK, or SMP-4100, Nihon-Koden Co. Ltd., Japan). Both the electrical and auditory stimuli were recorded as the trigger pulses used for subsequent off-line averaging of both the ERPs and SSR data.
3.3.3 RECORDING ANALOGUE DATA FOR EACH PARAMETER

3.3.3.1 Electroencephalogram (EEG)

EEG was recorded using Ag/AgCl disk electrodes placed on the scalp, according to the International 10-20 system with the reference of linked earlobes. The EEG analogue output was amplified through a bandpass filter of 0.53-120 Hz.

3.3.3.2 Electro-oculogram (EOG)

To monitor likely artifacts due to eye movements, EOG was recorded using a pair of small electrodes placed above and below the eye of one side.

3.3.3.3 Electromyogram (EMG)

EMG was recorded using pair(s) of surface electrodes on the triceps and/or biceps muscles of the preferred arm, mostly the right arm, and was amplified through a bandpass filter of 5.3-1500 Hz.

3.3.3.4 Sympathetic skin response (SSR)

SSR was recorded using Ag/AgCl disk electrodes placed on both the palmar and dorsal sites of non-preferred hand, mostly the left hand, and was amplified through a bandpass filter of 0.53-1500 Hz.

3.3.3.5 R-R intervals (only Experiment 3)

To examine R-R intervals as an autonomic response of the heart, ECG was recorded using three electrodes, one of which was placed on the sternum and the other two on each of the fifth ribs.

3.3.4 DATA STORAGE

All analog signals including the electrical signals converted from both electrical stimulation and auditory signals (WS) were recorded both on recording paper of an EEG recorder (1A97, NEC San-ei Co. Ltd., Japan, or EE1121A, NEC Medical Systems Co. Ltd., Japan) and on magnetic tape of a data recorder (XR-710, TEAC Co., Japan, or PC216Ax, Sony Precision Technology Inc., Japan).

3.3.5 DATA ANALYSES

Analog data of EEG, EOG, EMG and SSR stored on magnetic tape were
converted into digital data through an A/D converter installed on a personal computer (PC-9821 Xa7, NEC Co. Ltd., Japan), and analyzed with software (EPLYZER, Kissei Comtec Co. Ltd., Japan). Trials with either excessive muscle activity or eye blinks (detecting from EMG and EOG) were excluded from subsequent analyses in order to eliminate likely artifacts on the averaged waveforms of both ERPs and SSR.

3.3.5.1 EEG, N140 and P300

EEG analogue data were converted into digital data at a sampling rate of 200 or 500 Hz for 800 msec (sampling time ranging from 200 msec before the stimulus onset to 600 msec after the stimulus onset) and then averaged for each stimulus condition. The N140 and P300 components of ERPs were defined at peak amplitudes appearing in two different post-stimulus windows ranging from 120 to 160 and from 245 to 450 msec, respectively. The amplitudes of N140 and P300 were measured as relative potentials 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 amplitudes.

3.3.5.2 EMG

EMG data were converted into digital data at a sampling rate of 1000 Hz and used to determine the EMG-RT.

3.3.5.3 SSR

SSR data were converted into digital data at a sampling rate of 200 or 500 Hz with a sampling time of 3700 (Experiment 1), 4500 (Experiments 2 and 4), and 4700 msec (Experiment 3), and then averaged. The amplitude of SSR was measured as a peak-to-peak difference of the averaged waves. The latency of SSR was measured as the duration from the stimulus onset to the response onset determined at an initial rise from the 200-msec prestimulus baseline.

3.3.6 STATISTICS

Repeated measures analyses of variance (ANOVA) were performed on both the amplitudes and latencies of ERPs and SSR in each experiment. To decrease the experiment-wise error rate due to the repeated-measures design, a Greenhouse-Geisser adjustment to the degree of freedom was performed. The student's t-test was also used in part. A level of P<0.05 was accepted as indicating statistical significance.
CHAPTER 4 EXPERIMENTS

4.1 EFFECTIVENESS OF THE STIMULUS NOVELTY AND THE TASK RELEVANCE OF TARGET STIMULUS ON ELICITATION OF SYMPATHETIC SKIN RESPONSE (EXPERIMENT 1)

4.1.1 INTRODUCTION

Because SSR is elicited by novel, deviant and unexpected (surprising) stimuli, it reflects the peripheral neural function of orienting response, supported by simultaneous recording of the P300 component (P3a or novelty P3) of ERPs from the scalp. This response showed habituation (weakening or displacement of waveforms) with repetition of stimulus presentation and prolongation of test time. In addition, the SSR is apparently elicited when subjects are required to perform a voluntary movement to the given stimuli. Thus, it is hypothesized that there are two types of SSR. One is involuntarily (automatically) elicited as OR by the novel (or deviant) stimulus with P3a or novelty P3. The other is voluntarily elicited by a task-relevant stimulus (which requires subjects to produce a motor response) with the elicitation of P3b. The novel stimuli (which are usually presented with a low probability) are thought to be processed in the automatic mode of the brain, having a novel nature. On the other, the task-relevant stimuli are processed in the controlled mode that requires the attentional resources of the subjects and has the nature of task relevance.

In this experiment, the effectiveness of the stimulus novelty and the task relevance on evoking SSR was examined. The present experiment used a three-stimulus oddball paradigm (Pfefferbaum et al., 1984; Hiramatsu et al., 1985a; Hiramatsu et al., 1986). Hiramatsu et al. (1985a; Hiramatsu et al., 1986) and Pfefferbaum et al. (1984) have proposed, from experiments using the three-stimulus oddball paradigm, that the effects of the stimulus novelty and the task relevance on P300 can be evaluated separately by making a comparison between the two types of P300 (i.e., target- and nontarget-P300). Accordingly, the effects of stimulus novelty and task relevance on elicitation of SSR will also be examined in this experiment using the three-stimulus oddball paradigm.

In addition to the P300 components, the N140 component of ERPs was also measured in this experiment to assess the attentional level of the subjects for the two types
of rare stimuli (for more details, see Section 3.1.1).

4.1.2 METHODS

4.1.2.1 Subjects

Twelve neurologically normal volunteers (eight males and four females), aged from 21 to 29 years, participated in this experiment. Informed consent was obtained from each participant. The experimental settings were as mentioned in Section 3.3.1.

4.1.2.2 Recordings of EEG, EMG, and SSR

The recordings of EEG, EOG, EMG, and SSR were as mentioned in Section 3.3.3. Ag/AgCl disk electrodes were placed on F3, Fz, F4, C3, Cz, C4, and Pz for EEG recording. EMG was recorded using a pair of surface electrodes on the triceps muscle of the right arm. To record SSR, Ag/AgCl disk electrodes were placed on both palmar and dorsal sites of the left hand. Electrical stimulation generated using three electrical stimulators was delivered to either the index, middle, or little finger of the right hand. All analog signals including the electrical signals of each stimulus were recorded both on recording paper fed from an EEG recorder and on magnetic tape of a data recorder.

4.1.2.3 Procedures

Electrical stimuli were delivered in random order to either the index, middle, or little finger, which were assigned as the target, nontarget, and standard stimulus, respectively. The probabilities of these three stimuli were 0.1, 0.1, and 0.8, for the target, nontarget, and standard, respectively.

Experiments were performed under two conditions. In one condition (attend condition), subjects were instructed to respond to the target stimuli by extending the right elbow joint to press down on the upper plate as quickly as possible, whereas they were asked to ignore the other stimuli. For the other condition (ignore condition), the subjects were instructed to ignore any type of stimuli without any movement. Each condition consisted of 70 trials with various intertrial intervals ranging from 3 to 5 sec. The subjects performed three blocks of 70 trials under each condition, for a total of six experimental sessions. These six sessions were performed in an order counterbalanced between subjects.
4.1.2.4 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 500 Hz through an A/D converter installed on a personal computer (see Section 3.3.5). Digital data were analyzed with signal-processing software. Converted EEG data were averaged over 16 trials for both target and nontarget stimuli and were averaged over 50 trials for standard stimuli. The peak latency and amplitude of N140 and P300 components were defined as shown in Section 3.3.5.1. SSR data were converted for 3700 msec (ranging from 200 msec before the stimulus onset to 3500 msec after the stimulus onset) and averaged over 16 trials for both target and nontarget stimuli.

4.1.2.5 Statistics

Three-way ANOVAs were performed on the amplitudes and latencies of N140 and P300 for the following repeated-measures factors: conditions (C; attend and ignore), stimuli (S; target, nontarget, and standard) and electrodes (E; F3, Fz, F4, C3, Cz, C4, and Pz). 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 amplitudes of SSR between target and nontarget stimuli in the attend condition alone, because SSR did not appear for the ignore condition. In addition, difference waveforms were calculated by subtracting the waveform obtained for the standard stimulus from that for the either target or nontarget stimuli, resulting in two types of difference waveforms.

4.1.3 RESULTS

Figure 1 and Figure 2 show grand average waveforms of ERPs in the ignore (Figure 1) and attend (Figure 2) conditions.

4.1.4 N140 COMPONENTS

At all electrode sites, N140 components appeared for all types of stimuli in both conditions (Figure 1 and Figure 2). For the amplitudes of N140 (Table 1), the main effect for stimuli was significant (S; F=7.072, P<0.01), with the N140 amplitudes for both target and nontarget stimuli being significantly larger than that for standard stimulus (target, P<0.05; nontarget, P<0.01). The main effects for both conditions and electrodes were also significant but also significantly interacted with each other (C*E; F=5.636, P<0.01).
Subsequent simple main effect tests on the condition-electrode interaction revealed significant simple main effects for conditions at all electrode sites (F3, Fz, F4, P<0.01; C3, Cz, C4, Pz, P<0.001), with the amplitudes in the attend condition being larger than those in the ignore condition. The simple main effects for electrodes were significant for both the ignore (F=3.656, P<0.05) and attend conditions (F=6.642, P<0.01). Contrast tests were calculated among the electrode sites for both the ignore and attend conditions. For the ignore condition, the N140 amplitudes at both Fz and Cz were significantly larger than that at Pz (Fz, P<0.05; Cz, P<0.05), while the amplitudes at all contralateral sites (F3 and C3) did not differ from those at ipsilateral sites (F4 and C4). For the attend condition, the N140 amplitudes at both Fz and Cz were significantly larger than that at Pz (Fz, P<0.01; Cz, P<0.001). The amplitude at the ipsilateral site (C4) was significantly larger than that at the contralateral site (C3) (P<0.05).

For the N140 latencies (Table 2), the main effect for electrodes was significant (E; F=11.578, P<0.001). Contrast tests were then calculated among electrode sites. The results were as follows: i) the mean N140 latency at C3 was shorter than that at C4 (P<0.01); ii) the mean N140 latency at Cz was shorter than those at Fz and Pz (Cz vs. Fz, P<0.001; Cz vs. Pz, P<0.01).

4.1.4.1 P300 components

No typical P300 components appeared for either type of stimulus in the ignore condition, nor standard stimuli in the attend condition (Figure 1 and Figure 2). Two-way ANOVAs were performed on both the amplitudes and latencies of P300 components for both target and nontarget stimuli in the attend condition.

For the amplitudes of P300 (Table 3), the main effects for both stimuli and electrodes were significant but they also significantly interacted with each other (S*E; F=12.126, P<0.001). Subsequent t-tests performed between the two stimuli at each electrode site revealed that the P300 amplitude for target stimuli was significantly larger than that for nontarget stimuli at each site of C3, C4, and Pz (P<0.001). The simple main effect for electrodes was significant both for target (F=21.372, P<0.001) and nontarget stimuli (F=10.513, P<0.001). Contrast tests were then calculated among the electrode sites for both target and nontarget stimuli. For target stimuli, the P300 amplitude at Pz was significantly larger than those at the other electrode sites (P<0.01). For nontarget stimuli, the P300 amplitudes at both Cz and Pz were significantly larger than those at the other
electrode sites (P<0.05).

For the P300 latencies (Table 4), the main effects for both stimuli (S; F=16.228, P<0.01) and electrodes (E; F=3.802, P<0.05) were significant. Subsequent t-tests for stimuli revealed that the P300 latency for target stimuli was significantly shorter than that for nontarget stimuli (P<0.01). Contrast tests for electrodes revealed that the P300 latencies at both Cz and Pz were significantly shorter than that at Fz (Cz vs. Fz, P<0.05; Pz vs. Fz, P<0.01).

4.1.4.2 Difference waves

Difference waves in the ignore condition (Figure 3) showed slight shifts toward negative potentials (negative shifts) for both target and nontarget stimuli. The shifts rose at about 100 msec after the stimulus onset for both target and nontarget stimuli (thus corresponding to the N140 component), but these shifts did not significantly differ in size between the two. In the attend condition (Figure 4), such negative shifts appeared for both target and nontarget stimuli. For target stimuli, a sharp negative deflection also appeared at about 240 msec and this was then followed by a large positive shift (corresponding to the P300 component). Such a negative shift was most remarkable at Cz. For nontarget stimuli, moderate negative shifts arose at about 200 msec and were maintained until around 300 msec. A positive peak then appeared at about 450 msec.

4.1.4.3 SSR

None of the stimulus types in the ignore condition elicited typical SSR waveforms, whereas both target and nontarget stimuli in the attend condition elicited SSR (Figure 5). Student's paired t-tests were performed on the amplitudes and latencies of SSR between the two stimuli in the attend condition (Table 5). The amplitude of SSR for target stimuli was significantly larger than that for nontarget stimuli (P<0.001). The latency of SSR for target stimuli was significantly shorter than that for nontarget stimuli (P<0.01). However, it is difficult to discuss the difference in SSR latencies, because the SSR response waves showed an exponential slope at their onset and this caused a problem in identifying the correct SSR latencies. Therefore, discussions are focussed on the amplitude of the SSR which was evoked in the attend condition.
Figure 1: The waveforms of ERPs (grand average) for the standard, nontarget, and target stimuli in Ignore condition.
Figure 2: The waveforms of ERPs (grand average) for the standard, nontarget, and target stimuli in Attend condition.
Table 1: The amplitudes of N140 (μV) for the standard, nontarget, and target stimuli in Ignore and Attend conditions.

Note gives a summary of the ANOVAs for both significant effect for stimuli (S) and interaction between conditions and electrodes (C*E) on the N140 amplitudes.

| Electrode sites | Standard | | Nontarget | | Target | |
|-----------------|----------|-----------------|----------|-----------------|----------|
|                 | Mean     | SD              | Mean     | SD              | Mean     | SD              |
| Ignore          |          |                 |          |                 |          |                 |
| F4              | -3.147   | 2.163           | -4.743   | 2.227           | -4.152   | 3.747           |
| C3              | -2.716   | 2.069           | -3.750   | 2.348           | -2.620   | 3.318           |
| Cz              | -2.833   | 2.526           | -3.981   | 2.544           | -3.784   | 3.467           |
| C4              | -3.310   | 1.961           | -4.808   | 2.942           | -4.276   | 2.711           |
| Pz              | -1.551   | 2.197           | -2.583   | 3.314           | -2.368   | 2.540           |
| Attend          |          |                 |          |                 |          |                 |
| F4              | -7.622   | 5.359           | -9.813   | 5.288           | -8.950   | 5.642           |
| C3              | -5.820   | 3.545           | -7.788   | 3.924           | -7.072   | 4.021           |
| Pz              | -4.648   | 4.131           | -6.337   | 4.078           | -5.743   | 3.697           |

Note: F=7.072, P<0.01, for Stimuli
      : F=5.636, P<0.01, between Conditions and Electrodes
Table 2: The latencies of N140 (msec) for the standard, nontarget, and target stimuli in Ignore and Attend conditions. Note gives a summary of the ANOVAs for a significant main effect for stimuli (S) on the N140 latencies.

<table>
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<th>Electrode sites</th>
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<th>Nontarget Mean</th>
<th>SD</th>
<th>Target Mean</th>
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<td>11.26</td>
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Note: F=11.578, P<0.001, for Stimuli
Table 3: The amplitudes of P300 (μV) for the nontarget and target stimuli in Attend condition.
Note gives a summary of the ANOVAs for a significant interaction between stimuli and electrodes (S*E) on the P300 amplitudes

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>Nontarget Mean</th>
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<th>Target Mean</th>
<th>Target SD</th>
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Note: F=12.126, P<0.001, between Stimuli and Electrodes
### Table 4: The latencies of P300 (msec) for the nontarget and target stimuli in Attend condition.

Note gives a summary of the ANOVAs for significant main effect for both stimuli (S) and electrodes (E) on the P300 latencies.

<table>
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<tr>
<th>Electrode sites</th>
<th>Nontarget Mean</th>
<th>Nontarget SD</th>
<th>Target Mean</th>
<th>Target SD</th>
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<td>37.02</td>
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<td>65.80</td>
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Note: $F=16.228$, $P<0.001$, for Stimuli

$F=3.802$, $P<0.05$, for Electrodes
Figure 3: The difference waveforms of ERPs (grand average) for the nontarget and target stimuli in Ignore condition.
Difference Wave; ATTEND condition

Figure 4: The difference waveforms of ERPs (grand average) for the nontarget and target stimuli in Attend condition.
Figure 5: The waveforms of SSR for the nontarget and target stimuli in Ignore and Attend conditions.
Table 5: The amplitudes (μV) and latencies (sec) of SSR for the nontarget and target stimuli in Attend condition. Astarisks indicate statistical significance for the differences between nontarget and target stimuli.

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<th>Target</th>
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<td>Amplitude**</td>
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<tr>
<td>Latency *</td>
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<td>1.462</td>
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**: P<0.001
*: P<0.01
4.1.5 DISCUSSION

The purpose of this experiment was to examine the effectiveness of the stimulus novelty and the task relevance on elicitation of SSR. It has been suggested (e.g., Mimori & Tanaka, 1992; Arunodaya & Taly, 1995) that SSR reflects in part the level of attention paid by subjects to the stimuli used in evoking SSR. First, therefore, the level of subjects' attention paid to the given stimuli was examined by making comparisons of N140 components of ERPs both between the two conditions (i.e., ignore and attend conditions) and between the two rare stimuli (i.e., the target and nontarget). Second, the stimulus nature of both novelty and task relevance in the two rare stimuli was examined in terms of the results of P300. Finally, according to these examinations on ERPs, the effects of both stimulus novelty and task relevance on elicitation of SSR are discussed.

The amplitudes of N140 for all types of stimuli in the attend condition were larger than those in the ignore condition, with the N140 amplitudes at both frontal and central sites being dominant compared with that at parietal site. This implies that the attentional level of the subjects was higher in the attend condition than in the ignore condition (Desmedt & Robertson, 1977; García-Larrea et al., 1995; Hatta et al., 1997). Moreover, the N140 amplitude (indicating the level of subjects' attention) for the nontarget stimuli appeared similar to that for the target stimuli, which were both larger than that for standard stimuli. As these two rare stimuli were given to adjacent fingers, it must have been difficult for the subjects to discriminate between them. It is therefore suggested that the subjects' attention may probably be directed equally to both target and nontarget stimuli (Desmedt & Tomberg, 1989; Hatta et al., 1997).

In this experiment, rare nontarget stimuli were presented with a low probability (0.1) and required the subjects to ignore them without any motor response. Thus, the rare nontarget stimuli should have been characterized by the nature of novelty, automatically evoking the early subcomponent of P300 (i.e., either P3a or novelty P3). The target stimuli were also presented at the same probability as that of the nontarget stimuli, indicating that the target stimulus also had the nature of novelty. Furthermore, because the target stimuli required subjects to respond to them with a voluntary movement, the target stimuli must have been characterized by the nature of task relevance as well as novelty. Picton (1992) suggested that such task-relevant stimuli evoke the late subcomponent of P300, that is, P3b. In the present experiment, the target stimuli presented under the attend condition resulted in evocation of the late P300 subcomponent (target-P300) alone. The late P300
component seems to be identical to the P3b, because 1) the P300 subcomponent was generated by both task-relevant and rare target stimuli and 2) the amplitude of the subcomponent was predominant at parietal site. P3b is suggested to reflect attention-demanding, controlled processing of given stimuli in the brain (Halgren & Marinkobic, 1995) and its amplitude is thought to be proportional to the amount of attentional resources that are allocated to given tasks by subjects (Picton, 1992). Therefore, under the target stimuli in the present experiment, the subjects’ information-processing mode must have been that of task-relevant, controlled processing.

In addition, the results for target stimuli showed a negative shift appearing in difference waves at around 240 msec after the stimulus onset. The negative shift is considered to correspond to the somatosensory N250 (Kekoni et al., 1996; Kekoni et al., 1997, see Appendix B). The somatosensory N250 is generally evoked by rare target stimuli when subjects are asked to detect (rather than ignore) them, reflecting conscious detection of target stimuli (Kekoni et al., 1996; Kekoni et al., 1997). Therefore, the occurrence of negative shifts in difference waves also indicates that the target stimuli activated task-relevant, controlled information processing, i.e., conscious target detection.

For rare nontarget stimuli, neither P3a nor novelty P3 (i.e., the early subcomponent of P300) was elicited. Instead, the late subcomponent of P300 (nontarget-P300) appeared. Occurrence of the nontarget-P300 (with extended latency) implies that the time spent for stimulus evaluation (Kutas et al., 1977) and/or updating of cognitive context (Donchin & Coles, 1988) for nontarget stimuli is longer than that for target stimuli. The results also showed that the amplitude of nontarget-P300 was quite similar to that of target-P300. This implies that the amount of attentional resources of the subjects (Picton, 1992) used for information-processing of nontarget stimuli was equivalent to that for target stimuli, suggesting that attentional resources were allocated to information processing of nontarget stimuli as well as target stimuli. It is therefore suggested that the nontarget stimuli may not be processed in automatic mode but in the controlled mode of information processing. The type of controlled mode of information processing which is specific for nontarget stimuli may differ from that for target stimuli, because both scalp topography and latency of nontarget-P300 appeared quite different from those of the target-P300 (This was also suggested by Pfefferbaum & Ford, 1988, Pfefferbaum et al., 1985, and Simson et al., 1977).

Collectively, both the target and nontarget stimuli presented in this experiment
may be processed in the task-relevant, controlled processing mode rather than the automatic mode. This is consistent with the fact that amplitudes of N140 for nontarget stimuli appeared similar to that for target stimuli, as already described.

The SSR is generally recorded in a clinical test with unexpected, uncertain, and surprising stimuli, accompanying the occurrence of either P3a or novelty P3 (Miyakawa et al., 1992; Deguchi et al., 1996; Knight, 1996). It has therefore been thought that the SSR and other EDAs (e.g., skin potential response, SPR, and skin conductance response, SCR) are primarily caused by a stimulus nature of novelty, reflecting a type of orienting response mediated by the autonomic nervous system. According to this notion, it was predicted in the present experiment that the two rare stimuli (i.e., the target and nontarget) should elicit SSR as well as P3a (or novelty P3) because of the rare presentation of these rare stimuli in the experiment.

Nevertheless, these two rare stimuli elicited neither P3a nor novelty P3, indicating that these two rare stimuli may not be processed in the automatic mode of information processing. Furthermore, for SSR, only a small SSR wave appeared for nontarget stimuli, although a large SSR arose for the target stimuli. This implies that the two rare stimuli are not simply processed in the automatic processing mode, despite the nature of stimulus novelty inherent in these two rare stimuli.

Rather, the nature of task relevance, which is inherent in the two rare stimuli (particularly in the target stimulus), may be a primary cause of the occurrence of SSR in the present experiment. The task-relevance nature of target stimulus is likely characterized by the specific signal value or meaning (Roth, 1983, see Chapter 2; Johnson, 1986; Johnson, 1988a; Johnson, 1993) of the target stimulus which requires the subjects to perform a voluntary movement (i.e., pressing a button) as the response to each target stimulus (Roth, 1983). Such a signal value/meaning requiring motor responses to the target stimuli may be responsible for raising large SSR waves as shown in both a previous study (Siddle et al., 1979, see Section 2.1.3.1.3) and the present experiment. Specifically, neurophysiological evidence has recently suggested that when the brain areas relating to voluntary movement and attention are activated, some electrodermal responses (e.g., SCR, SPR, and SSR) are also elicited at the same time. Sequeira and Roy (1993) have shown that electrical stimulation of the pericruciate area (primary motor and supplementary motor areas, in humans) of the cat elicits larger SPRs compared with the SPRs caused by stimulation applied to the parietal area (somatosensory areas) (see Chapter 2). Fredrikson
et al. (1998) also suggested in their study using positron emission tomography (PET) (see Section 2.1.2.3.3) that EDAs (SPR, SCR, and SSR) seem to reflect movement-related processes which are cognitively or emotionally mediated. Their PET data revealed that when cerebral blood flow in both the primary motor area and the anterior cingulate cortex increased, EDAs were elicited. The primary and supplementary motor areas are widely accepted to play an important role for motor production. The former generates motor commands descending to skeletal muscles, resulting in the motor commands to contract the skeletal muscles. The latter provides detailed motor programs, which enable subjects to perform appropriate movements. The cingulate cortex acts as part of an attentional system that controls both the endocrine and autonomic functions (c.f., Devinski et al., 1995). These findings therefore imply that the functions of movement- and attention-related brain areas (i.e., the primary and supplementary motor areas and the cingulate cortex) may control the EDAs. Accordingly, it is likely that the SSR may have been clearly evoked under target stimuli conditions because of the movement-related, controlled (i.e., attention-demanding) mode of information processing.

In contrast, for nontarget stimuli, the task-relevance nature is likely characterized by a signal value/meaning different from that for target stimulus, because the nontarget stimuli require the subjects to ignore, rather than respond to, the stimuli. The subjects attended to the nontarget stimuli (which was supposed to be ignored) as well as they did to the target stimuli (these were indicated by the large N140 amplitudes). However, the subjects were asked not to respond to the nontarget stimuli. This implies that the subjects consciously detect the nontarget stimuli just as well as the target stimuli but voluntarily stop any movement (i.e., voluntarily ignore the stimuli). Such ‘attend-ignore’ process for the nontarget stimuli should have different task-relevance (signal value/meaning) compared with the ‘attend-respond’ process for the target stimuli. This is supported by the results of both the large N140 amplitudes and the extended P300 latencies for nontarget stimuli. As described in the previous part of this section, it is suggested that the attend-ignore process of information processing, which is specific to nontarget stimuli, may differ from the attend-respond process for target stimuli. These processes of information processing will be discussed in a later section (Experiment 4) dealing with experiments using a Go/NoGo paradigm, i.e., the attend-respond process is assumed to be activated in the Go-P300 and the attend-ignore process in the NoGo-P300 (e.g., Simson et al., 1977; Pfefferbaum et al., 1985; Pfefferbaum & Ford, 1988; Roberts et al., 1994).
In conclusion, it is suggested that SSR evoked during a voluntary movement is enhanced when the given stimulus is processed in the controlled processing mode; that is, attention-demanding, task-relevant information processing (e.g., conscious target detection and voluntary motor execution). It is also suggested that SSR is not evoked by the novelty of the stimulus processed in the automatic processing mode. In addition, the SSRs for both target and nontarget stimuli may reflect respective electrodermal responses for response production (Go) and response inhibition (NoGo).
4.2 **EFFECTS OF VOLUNTARY MOVEMENTS ON SYMPATHETIC SKIN RESPONSE UNDER ATTENTIVE CONDITIONS (EXPERIMENT 2)**

**4.2.1 INTRODUCTION**

The results of Experiment 1 suggested that SSR arises when a given stimulus is processed in the controlled, rather than the automatic, processing mode (which is assumed when P3b components of ERPs appear) during voluntary movement, such as a reaction time task. The controlled processing mode is primarily activated in the processing of task-relevant, target stimuli, such as the stimuli requiring subjects to either consciously detect each of them from other task-irrelevant, nontarget stimuli or respond to them by some motor production. Therefore, the task-relevant, target stimuli include two factors, conscious target detection and motor production. It is unclear which factor, target detection or motor production, is important to elicitation of the SSR. For example, when subjects are asked to count in mind the number of target stimuli, the subjects should be attentive to detect each target stimulus in the stimulus sequence. Such an effect of target stimuli on the subjects' attention is termed the target effect. The target effect is not only limited to occur in counting tasks but in reaction time (RT) tasks. Although the P3b is elicited by target stimuli in both tasks, the amplitudes of P3b recorded under RT tasks differ from those recorded under counting tasks. It has been suggested that the requirement of motor responses involved in RT tasks may provide some specific meaning to the target stimulus (stimulus meaning). If this is the case, the SSR might be affected by the stimulus meaning relating to motor production. This was examined in Experiment 2 (for more details, see Section 3.1.2).

**4.2.2 METHODS**

**4.2.2.1 Subjects**

Ten neurologically normal volunteers (eight males and two females), aged from 20 to 29 years, participated in this experiment. Informed consent was obtained from each participant. Experimental settings were as mentioned in Section 3.3.1.

**4.2.2.2 Recordings of EEG, EMG, and SSR**

The recordings of EEG, EMG, and SSR were the same as those used in
Experiment 1 (see Section 3.3.3). Nine Ag/AgCl disk electrodes for recording EEG were placed on F3, Fz, F4, C3, Cz, C4, P3, Pz and P4. EMG was recorded using two pairs of surface electrodes placed on both the triceps and the biceps muscles of the right arm. Electrical stimulus was delivered to either the index or little finger of the right hand. All analog signals including the electrical signals of each stimulus were recorded both on recording paper using an EEG recorder and on the magnetic tape of a data recorder.

4.2.2.3 Procedures

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 interval (3 sec). In the count condition the subjects were asked to count the number of target stimuli while in the reaction condition they were asked to perform elbow extension responses as quickly as possible when they perceived target stimuli. 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.

4.2.2.4 Analyses of N140, P300, and SSR

The measurements of ERPs and SSR were almost the same as those used in the previous Experiment 1 (see Section 3.3.5). EEG and SSR analog signals were converted into digital data at a sampling rate of 200 Hz. Converted EEG data were averaged over 16 samples for target stimuli and over 75 samples for standard stimuli. SSR data were converted for 4500 msec (ranging from 0 msec to 4500 msec after the stimulus onset) and were averaged over 16 samples with target stimuli and 75 samples with standard stimuli. The amplitude of SSR was measured as shown in Section 3.3.5.3.

4.2.2.5 Statistics

Three-way ANOVAs were performed on each of the amplitudes and latencies of N140 for the following repeated-measures factors: conditions (C; reaction and count), stimuli (S; target and standard) and electrodes (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 conditions (C) and electrodes (E) factors because the P300 components apparently
arose when the target stimuli were presented but not when the standard stimuli were presented. 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.

### 4.2.3 RESULTS

In the count condition, the subjects accurately answered the number of target stimuli. Figure 6 and Figure 7 show typical recordings of both ERP and SSR under each condition in one subject.

#### 4.2.3.1 N140 components

For the amplitudes of N140 (Table 6), 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 7), 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 ($P<0.01$).

#### 4.2.3.2 P300 components

P300 components of ERPs clearly appeared at all of the electrode sites for target stimuli but did not for standard stimuli (Figure 6). For the P300 amplitudes (Figure 8, Table 8), 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 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 8, Table 9), the main effect for conditions was significant (F=12.968, P<0.01). A subsequent paired t-test revealed that P300 latency in the reaction condition was significantly shorter than that in the count condition (P<0.01).

4.2.3.3 SSR

In both conditions, target stimuli evoked clear SSR waveforms (Figure 7), 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 10).
Figure 6: Typical recordings of ERPs for the standard and target stimuli in Count and Reaction conditions.
Figure 7: Typical recordings of SSRs for the target stimuli in Count and Reaction conditions.
Table 6: 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 conditions (C) and electrodes (E) on the N140 amplitudes.

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</tr>
<tr>
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<tr>
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Note: F=10.858, P<0.01, for Conditions
      : F=4.802, P<0.05, for Electrodes
Table 7: 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 electrodes (E) on the N140 latencies.

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

Note: F=10.649, P<0.001, for Electrodes
Figure 8: 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 8: 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 electrodes (E) on the P300 amplitudes.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>Count Mean</th>
<th>SD</th>
<th>Reaction Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>F3</td>
<td>11.166</td>
<td>4.049</td>
<td>11.725</td>
<td>4.260</td>
</tr>
<tr>
<td>Fz</td>
<td>10.129</td>
<td>3.912</td>
<td>11.618</td>
<td>3.682</td>
</tr>
<tr>
<td>C3</td>
<td>14.619</td>
<td>3.957</td>
<td>16.151</td>
<td>2.414</td>
</tr>
<tr>
<td>Cz</td>
<td>17.353</td>
<td>5.254</td>
<td>16.978</td>
<td>3.976</td>
</tr>
<tr>
<td>C4</td>
<td>14.751</td>
<td>3.446</td>
<td>15.981</td>
<td>3.406</td>
</tr>
<tr>
<td>P3</td>
<td>17.177</td>
<td>5.266</td>
<td>19.290</td>
<td>2.989</td>
</tr>
<tr>
<td>Pz</td>
<td>17.904</td>
<td>5.274</td>
<td>18.963</td>
<td>3.376</td>
</tr>
<tr>
<td>P4</td>
<td>16.846</td>
<td>5.711</td>
<td>18.752</td>
<td>4.293</td>
</tr>
</tbody>
</table>

Note: F=28.342, P<0.001, for Electrodes
Table 9: 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 conditions (C) on the P300 latencies.

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

Note: F=12.968, P<0.01, for Conditions
Table 10: The amplitudes of SSR (mV) to the target stimuli in Count and Reaction conditions.
Astarisk shows a significant difference of SSR amplitudes between the two conditions.

<table>
<thead>
<tr>
<th></th>
<th>Count</th>
<th></th>
<th>Reaction</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>SSR*</td>
<td>0.417</td>
<td>0.126</td>
<td>2.393</td>
<td>0.757</td>
</tr>
</tbody>
</table>

*: P<0.001
4.2.4 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 (Picton, 1992). 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 (e.g., Desmedt & Tomberg, 1989; Allison et al., 1992) or the central area (the secondary somatosensory cortex, Tarkka et al., 1996) 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 (arousal state) of the subjects was higher in the reaction condition than in the count condition (c.f., Desmedt & Robertson, 1977; García-Larrea et al., 1995; Hatta et al., 1997).

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 (Kutas et al., 1977) and updating the cognitive context, such as updating the memory of a given stimulus after evaluating incoming information of the stimulus (Donchin & Coles, 1988), was shortened in reaction condition. Some researchers (Johnson, 1986; Barrett et al., 1987; 1988a) showed that P3b clearly appeared when target stimuli were presented in both count and reaction conditions. Barrett et al. (1987) 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 (under the controlled mode) 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 (Kutas et al., 1977) and that P300 is sensitive to stimulus evaluation but not to response selection processes (Duncan-Johnson & Kopell, 1981; McCarthy & Donchin, 1981). Although it is therefore necessary to further examine both the significance of target stimuli (i.e., 'stimulus meaning,' Johnson, 1986; Johnson, 1988a; Johnson, 1993) 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 (1987) showed that P300 amplitudes appeared larger for a button-press response than for a count response. Johnson (Johnson, 1986; Johnson, 1988a; Johnson, 1993) 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 (see Section 2.2.2.2.4). 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. (1987) and Johnson (Johnson, 1986; Johnson, 1988a; Johnson, 1993), 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 (Picton, 1992). 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.

EDAs, such as SSR, skin conductance response (SCR), and skin potential response (SPR), have often been reported to appear when a novel stimulus is presented to subjects (e.g., Deguchi et al., 1996; Knight, 1996). Therefore, SSR is thought to be sensitive to the novelty of stimulus and is processed in the automatic mode of information processing (Miyakawa et al., 1992; Knight, 1996; Lagopoulos et al., 1998). In this experiment, the target stimuli were presented as 20% of all the given stimuli in both count and reaction conditions. However, neither P3a nor novelty P3, which should have been elicited by the nature of stimulus novelty, appeared. This therefore indicates that the
nature of stimulus novelty was not a primary characteristic of the target stimuli in either condition used in the present experiment and that the elicitation of SSR under both the count and reaction conditions may not have been mediated by stimulus novelty. The results of the previous experiment (Experiment 1) also suggested that SSR was hardly affected by the novelty of stimulus, which is supposed to be processed in the automatic processing mode. This is also consistent with the present results of SSR.

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 (Lindsley, 1960). The arousal states of subjects are well known to primarily influence the elicitation of SSR (Mimori & Tanaka, 1992; Arunodaya & Taly, 1995). 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, 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. (1979) 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,' Johnson, 1986; Johnson, 1988a) is an important determinant of EDA (see Section 2.1.3.1.3 for the details). Bernstein and Taylor (1979) 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 (1983) suggested that the 'signal value' (which is identical to 'stimulus value' as one of the variables of stimulus meaning, Johnson, 1986; Johnson, 1988a) 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. (1998a) reported that SSR rose together with the bereitschaftspotential (Kornhuber & Deecke, 1965) and the event-related desynchronization (ERD) of EEG-alpha waves (Pfurtscheller & Aranibar, 1977) preceding self-paced voluntary movements, suggesting that information-processing relating to motor preparation affected the elicitation of SSR. The findings of Osada et al. indicate that activation of the brain regions (e.g., the primary and supplementary motor areas) in programming motor command for a voluntary movements (Defebvre et al., 1994; Vidal et al., 1995) also activates the autonomic responses. Moreover, Sequeira and Roy (1993) showed that electrical stimulation at the pericruciate area (in humans, corresponding to the primary and supplementary motor areas) of the cat elicited larger SPRs compared with those caused by stimulation at the parietal area (in humans, the somatosensory areas). 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 nature of novelty is not a primary characteristic of the target stimuli in either the count or reaction condition, and that the elicitation of SSR under both count and reaction conditions is mediated by task-relevant nature of the target stimuli rather than by stimulus novelty. 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.
4.3 EFFECTS OF THE WARING SIGNAL USED IN A REACTION TIME PARADIGM ON SYMPATHETIC SKIN RESPONSE (EXPERIMENT 3)

4.3.1 INTRODUCTION

The results of the previous experiments (Experiments 1 and 2) suggested that SSR arises when a given stimulus is processed in the movement-related, controlled mode of information processing (which is assumed to be activated when the P3b component of ERPs appears) during voluntary movement. A question which arises from the discussions in the previous experiments is whether the stimulus evaluation (i.e., stimulus identification, decision-making, and context updating) and/or movement-related systems (i.e., response selection, response programming, and response execution) relating to the execution of voluntary movements (c.f. Hiramatsu et al., 1985a; Tadai et al., 1986) affect the elicitation of SSR.

The former is reflected in the latency of P3b, which is thought of as a useful index of processing time spent for stimulus evaluation. For the movement-related system, EMG-RT is usually used to evaluate the total time spent for the information processing of stimulus identification, response selection and programming, and the delivery of motor commands to the skeletal muscles which must be activated. Both P3b and EMG-RTs are well known to decrease in reaction-time tasks in which a warning signal/stimulus (WS) is given to subjects prior to the imperative signal/stimulus (IS). This can be explained in terms of both anticipation of the stimulus and preparation of voluntary movement during the WS-IS interval. Such a WS-IS paradigm has been used by a number of researchers (see Appendix A) to investigate the relationships between autonomic activities (e.g., HR, blood pressure, and skin conductance level) and cortical responses (e.g., the desynchronization of EEG and appearance of the contingent negative variation, CNV) taking place during the WS-IS intervals. These studies suggest that cortical excitation in both processes of the stimulus anticipation and motor preparation (these are reflected in the amplitude of CNV) activated the ascending reticular activating system (ARAS). Activation of ARAS should result in some enhancement of SSR, because ARAS is thought to control the frequency of sympathetic discharge. However, it is still unclear whether or not the SSR evoked by the IS changes during reaction-time tasks. This was examined in Experiment 3 (for more details, see Section 3.1.3).
4.3.2 METHODS

4.3.2.1 Subjects

Eight neurologically normal volunteers (six males and two females), aged from 21 to 25 years, participated in this experiment. Informed consent was obtained from each participant. The experimental settings were as described in Section 3.3.1.

4.3.2.2 Recordings of EEG, EMG, SSR, and ECG

The recordings of EEG, EMG, SSR, and ECG were made in the same way as shown in Section 3.3.3. Disk electrodes were placed at Fz, Cz, Pz, C3, and C4, respectively, for EEG measurements. EMG was recorded using a pair of surface electrodes on the triceps muscle of the right arm. To record SSR, Ag/AgCl disk electrodes were placed on both palmar and dorsal sites of the left hand.

An electrical stimulus was delivered to each of the index and little finger of the subjects' right hand. An auditory click tone (50 dB) was generated as a warning signal (WS) using an auditory stimulator and delivered to the subjects via headphones.

4.3.2.3 Procedures

After a 10-minute resting period, subjects performed two reaction-time tasks. One task was a typical oddball paradigm without a WS (oddball paradigm), and the other task with a WS (WS-IS paradigm). In the oddball paradigm, more than 100 electrical stimuli were delivered to either the index (target, 20%) or the little (standard, 80%) fingers. In the WS-IS paradigm, a warning click was given first and, 3 to 5 sec after, either the target (20%) or standard (80%) stimulus was randomly delivered as an imperative. The experimenter instructed the subjects to perform elbow extension responses in both paradigms. Each subject performed more than 100 trials with various interstimulus intervals ranging from 6 to 10 sec. The subjects were also instructed to ignore all of the standard stimuli in both paradigms. These two paradigms were performed in an order counterbalanced between subjects.

4.3.2.4 Analyses of N140, P300, EMG-RT, SSR, and R-R Intervals

ERPs and SSR were measured in almost the same way as in the previous experiments (see Section 4.1.2.4 and 4.2.2.4). Converted EEG data were averaged over 16 samples for target stimuli and over 70 samples for standard stimuli. EMG analog signals
Chapter 4 Experiments

were converted into digital data at a sampling rate of 1000 Hz. Analyzing the converted EMG data, the EMG-RT was measured (see Section 3.3.5.2). SSR data were converted for 4700 msec (ranging from 200 msec before the stimulus onset to 4500 msec after the stimulus onset) and were averaged over 16 samples with target stimuli and 70 samples with standard stimuli. For ECG recordings, three consecutive R-R intervals were measured prior to each of the target, warning, and imperative target stimuli, and each mean value was then calculated.

4.3.2.5 Statistics

Three-way ANOVAs were performed on the amplitude and latency data of both N140 and P300 for the following repeated-measures factors: paradigms (P; oddball and WS-IS), stimuli (S; standard and target) and electrodes (E; Fz, Cz, Pz, C3, and C4). The R-R intervals were also tested by one-way ANOVA with a repeated-measures factor (time; before target in oddball, before warning and imperative target signals in WS-IS paradigms). The Student's paired t-test was used to compare the effects of the two paradigms on both SSR and EMG-RT for the target stimulus only.

4.3.3 RESULTS

Figure 9 shows the averaged waveforms of ERPs for target stimuli in the two paradigms at each electrode site. The target stimuli consistently evoked P300 components of ERPs at all sites.

4.3.3.1 N140 components

For the amplitudes of N140 (Table 11), the main effects for both paradigms and stimuli were not significant but the main effect for electrodes was significant (F=5.930, P<0.01). Contrast tests were then calculated among electrode sites. The results revealed that the N140 amplitudes at both frontal (Fz) and central (Cz) electrode sites were significantly larger than those at the parietal site (Fz vs. Pz, P<0.01; Cz vs. Pz, P<0.001). The N140 amplitudes at C3 did not differ from those at C4.

For the latencies of N140 (Table 12), the main effect for paradigms was not significant but the main effect for stimuli was significant (F=10.834, P<0.05), with the N140 latencies for target stimuli being significantly shorter than those for standard stimuli. The main effect for electrodes was also significant (F=4.843, P<0.05). Contrast tests were then calculated among electrode sites. The results revealed that the N140 latencies at Fz
were longer than those at Cz and Pz (Fz vs. Cz, P<0.05; Fz vs. Pz, P<0.05). The N140 latencies at C3 did not differ from those at C4.

4.3.3.2 P300 components

For the P300 amplitudes (Table 13), the main effects for paradigms and stimuli were not significant whereas the interaction between stimuli and electrodes was significant (F=6.747, P<0.001). Subsequent simple main effect tests on the stimulus-electrode interactions revealed significant simple main effects for sites as follows: i) for the standard stimulus (F=13.568, P<0.001) the P300 amplitude at Cz was significantly larger than those at the other sites (Fz, P<0.001; Pz, P<0.01; C3, P<0.001; C4, P<0.01); ii) for the target stimulus (F=5.617, P<0.05) the P300 amplitude at Fz was significantly lower than those at the other sites (Cz, P<0.05; Pz, P<0.01; C4, P<0.05), except C3, and the P300 amplitude at Pz was significantly larger than that at C3 (P<0.05). The simple main effect for stimuli (target vs. standard) was significant at Pz alone (P<0.05) but not at other sites.

For the P300 latencies (Table 14), the main effects for paradigms (F=8.989, P<0.05) and stimuli (F=41.325, P<0.001) were significant: P300 latencies were significantly shorter in the WS-IS than in the oddball paradigm and for the target than for the standard stimulus.

4.3.3.3 SSR

In this study, most standard stimuli failed to evoke SSR. Figure 10 shows the averaged waveforms of SSR for target stimulus in both paradigms. The amplitudes and latencies of SSR did not significantly differ between the oddball and WS-IS paradigms (Table 15). In some subjects, the SSR amplitudes tended to decrease in the WS-IS paradigm.

4.3.3.4 R-R Intervals

R-R intervals prior to the target (oddball paradigm), warning, and imperative target stimuli (WS-IS paradigm) did not significantly differ from each other (Table 16).

4.3.3.5 EMG-RT

EMG-RT for target stimulus was significantly shorter in the WS-IS paradigm than in the oddball paradigm (P<0.05, Table 17).
Figure 9: The waveforms of ERPs (grand average) for the target stimulus in Oddball and WS-IS paradigms.
Table 11: The amplitudes of N140 (µV) for the standard and target stimuli in Oddball and WS-IS paradigms. Note gives a summary of the ANOVAs for a significant main effect for electrodes (E) on the N140 amplitudes.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>Standard Mean</th>
<th>SD</th>
<th>Target Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Oddball</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>-2.407</td>
<td>2.224</td>
<td>-3.775</td>
<td>2.753</td>
</tr>
<tr>
<td>C3</td>
<td>-2.207</td>
<td>2.068</td>
<td>-2.468</td>
<td>2.696</td>
</tr>
<tr>
<td>Cz</td>
<td>-2.771</td>
<td>2.853</td>
<td>-4.109</td>
<td>3.946</td>
</tr>
<tr>
<td>C4</td>
<td>-2.854</td>
<td>2.149</td>
<td>-3.501</td>
<td>2.936</td>
</tr>
<tr>
<td>Pz</td>
<td>-1.097</td>
<td>2.067</td>
<td>-1.960</td>
<td>2.707</td>
</tr>
<tr>
<td><strong>WS-IS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>-3.151</td>
<td>2.884</td>
<td>-3.771</td>
<td>2.211</td>
</tr>
<tr>
<td>C3</td>
<td>-2.393</td>
<td>1.764</td>
<td>-2.890</td>
<td>2.463</td>
</tr>
<tr>
<td>Cz</td>
<td>-3.098</td>
<td>2.675</td>
<td>-4.407</td>
<td>3.826</td>
</tr>
<tr>
<td>C4</td>
<td>-2.925</td>
<td>1.883</td>
<td>-3.087</td>
<td>2.499</td>
</tr>
<tr>
<td>Pz</td>
<td>-1.471</td>
<td>1.706</td>
<td>-1.598</td>
<td>2.920</td>
</tr>
</tbody>
</table>

Note: F=5.930, P<0.01, for Electrodes
Table 12: The latencies of N140 (msec) for the standard and target stimuli in Oddball and WS-IS paradigms. Note gives a summary of the ANOVAs for significant main effect for both stimuli (S) and electrodes (E) on the N140 latencies.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>Standard</th>
<th>Target</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td><strong>Oddball</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>150.625</td>
<td>9.039</td>
</tr>
<tr>
<td>C3</td>
<td>141.875</td>
<td>5.939</td>
</tr>
<tr>
<td>Cz</td>
<td>144.375</td>
<td>11.160</td>
</tr>
<tr>
<td>C4</td>
<td>146.875</td>
<td>9.978</td>
</tr>
<tr>
<td>Pz</td>
<td>140.625</td>
<td>11.783</td>
</tr>
<tr>
<td><strong>WS-IS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>151.250</td>
<td>8.345</td>
</tr>
<tr>
<td>C3</td>
<td>140.000</td>
<td>6.547</td>
</tr>
<tr>
<td>Cz</td>
<td>142.500</td>
<td>9.258</td>
</tr>
<tr>
<td>C4</td>
<td>146.250</td>
<td>7.906</td>
</tr>
<tr>
<td>Pz</td>
<td>146.250</td>
<td>8.763</td>
</tr>
</tbody>
</table>

Note: F=10.834, P<0.05, for Stimuli
     : F=4.843, P<0.05, for Electrodes
Table 13: The amplitudes of P300 (μV) for the standard and target stimuli in Oddball and WS-IS paradigms. Note gives a summary of the ANOVAs for a significant interaction between stimuli and electrodes (S*E) on the P300 amplitudes.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>Standard</th>
<th>Target</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td><strong>Oddball</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>4.90</td>
<td>1.06</td>
</tr>
<tr>
<td>C3</td>
<td>4.69</td>
<td>1.02</td>
</tr>
<tr>
<td>Cz</td>
<td>7.23</td>
<td>2.17</td>
</tr>
<tr>
<td>C4</td>
<td>5.52</td>
<td>1.63</td>
</tr>
<tr>
<td>Pz</td>
<td>5.54</td>
<td>2.07</td>
</tr>
<tr>
<td><strong>WS-IS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>5.49</td>
<td>0.93</td>
</tr>
<tr>
<td>C3</td>
<td>5.80</td>
<td>1.43</td>
</tr>
<tr>
<td>Cz</td>
<td>8.14</td>
<td>1.80</td>
</tr>
<tr>
<td>C4</td>
<td>6.50</td>
<td>1.43</td>
</tr>
<tr>
<td>Pz</td>
<td>6.21</td>
<td>1.67</td>
</tr>
</tbody>
</table>

Note: F=6.747, P<0.001, between Stimuli and Electrodes
Table 14: The latencies of P300 (msec) for the standard and target stimuli in Oddball and WS-IS paradigms. Note gives a summary of the ANOVAs for significant main effects for both paradigms (P) and stimuli (S) on the P300 latencies.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>Standard Mean</th>
<th>Standard SD</th>
<th>Target Mean</th>
<th>Target SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oddball</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>359.38</td>
<td>18.02</td>
<td>310.63</td>
<td>54.60</td>
</tr>
<tr>
<td>C3</td>
<td>360.00</td>
<td>17.93</td>
<td>309.38</td>
<td>39.50</td>
</tr>
<tr>
<td>Cz</td>
<td>355.00</td>
<td>14.88</td>
<td>311.25</td>
<td>44.54</td>
</tr>
<tr>
<td>C4</td>
<td>362.50</td>
<td>16.48</td>
<td>315.62</td>
<td>42.63</td>
</tr>
<tr>
<td>Pz</td>
<td>363.13</td>
<td>21.03</td>
<td>315.63</td>
<td>37.07</td>
</tr>
<tr>
<td>WS-IS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>350.00</td>
<td>19.46</td>
<td>269.38</td>
<td>34.69</td>
</tr>
<tr>
<td>C3</td>
<td>341.88</td>
<td>25.63</td>
<td>274.38</td>
<td>16.35</td>
</tr>
<tr>
<td>Cz</td>
<td>337.50</td>
<td>20.18</td>
<td>296.38</td>
<td>18.60</td>
</tr>
<tr>
<td>C4</td>
<td>348.13</td>
<td>20.52</td>
<td>281.88</td>
<td>16.02</td>
</tr>
<tr>
<td>Pz</td>
<td>351.25</td>
<td>25.18</td>
<td>286.25</td>
<td>15.06</td>
</tr>
</tbody>
</table>

Note: F=8.989, P<0.05, for Paradigms
F=16.168, P<0.01, for Stimuli
Figure 10: The waveforms of SSRs (grand average) for the target stimulus in Oddball and WS-IS paradigms.
Table 15: The amplitudes (mV) and latencies (sec) of SSR for the target stimuli in Oddball and WS-IS paradigms.

<table>
<thead>
<tr>
<th></th>
<th>Oddball</th>
<th></th>
<th>WS-IS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>Amplitude</td>
<td>1.07</td>
<td>0.68</td>
<td>0.67</td>
</tr>
<tr>
<td>Latency</td>
<td>1.439</td>
<td>0.084</td>
<td>1.412</td>
</tr>
</tbody>
</table>
Table 16: The R-R intervals (msec) prior to each stimulus (target and warning) in Oddball and WS-IS paradigms.

<table>
<thead>
<tr>
<th></th>
<th>Oddball</th>
<th></th>
<th>WS-IS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Target</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R-R interval</td>
<td>923</td>
<td>101</td>
<td>912</td>
</tr>
<tr>
<td></td>
<td>Warning</td>
<td></td>
<td>99</td>
</tr>
<tr>
<td>R-R interval</td>
<td>938</td>
<td>98</td>
<td></td>
</tr>
</tbody>
</table>

Note: The table includes the mean and standard deviation (SD) for R-R intervals prior to each stimulus in Oddball and WS-IS paradigms.
Table 17: The EMG-RT (msec) for the target stimuli in Oddball and WS-IS paradigms. 
Asterisk shows a significant difference in EMG-RT between the two paradigms.

<table>
<thead>
<tr>
<th></th>
<th>Oddball</th>
<th></th>
<th>WS-IS</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>EMG-RT*</td>
<td>298.78</td>
<td>48.69</td>
<td>265.17</td>
<td>51.79</td>
</tr>
<tr>
<td>*: P&lt;0.05</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
4.3.4 DISCUSSION

The purpose of this experiment was to examine the effects of warning signal (WS) on elicitation of SSR. The results of ERPs in both paradigms will be first discussed on the basis of the stimulus nature of the target stimuli that should be influenced by the WS. Following this, the effects of WS on elicitation of SSR will be discussed.

In both WS-IS and oddball paradigms, N140 components were clearly evoked by both standard and target stimuli. The amplitudes of N140 components were similar to each other for WS-IS and oddball paradigms and for target and standard stimuli, whereas N140 amplitudes were larger at the frontal and central electrode sites than at the parietal site. As mentioned previously (Experiment 2), either the frontal (e.g., Desmedt & Tomberg, 1989; Allison et al., 1992) or the central area (the secondary somatosensory cortex, Tarkka et al., 1996) is suggested to be the source area of N140 and to contribute to generating human attention and intention. The results for N140 therefore imply that the subjects may have been attentive to the given stimuli in both paradigms (c.f., Desmedt & Robertson, 1977; Garcia-Larrea et al., 1995; Hatta et al., 1997).

On the other hand, the latency of N140 components for target stimuli was shorter than that for standard stimuli. Hatta et al. (1997) showed that the latency of N140 at Cz and C3' (which locates at 2 cm posterior to C3) for target stimuli in a reaction time task was shorter than that in a counting task, suggesting that N140 may be related to motor production processes as well as attention. The shorter latency of N140 in the present result is therefore interpreted in terms of both subjects’ attention for detecting target stimuli among the standard stimuli and the requirement of motor responses to the target stimuli.

P300 components were evoked clearly by target stimuli but were not clear for the standard stimuli. The P300 component evoked by the target stimulus was identified as P3b (Squires et al., 1975b) because it was evoked by task-relevant, target stimuli and had maximal peaks at parietal sites (Picton, 1992). The latencies of P3b (as well as EMG-RTs) appeared shorter in the WS-IS paradigm than in the oddball paradigm. This indicates that the time spent for stimulus evaluation, such as stimulus identification (Kutas et al., 1977), decision-making (Desmedt, 1980), and context updating (i.e., updating the memory of the given stimulus after the evaluation of incoming information of the stimulus, see Donchin & Coles, 1988), was shortened in the WS-IS paradigm. In this case, the subjects probably anticipated the presentation of IS and made preparations for their motor responses to the
IS. In fact, after the completion of the experiment, most subjects introspectively reported that it was easier to respond to target stimuli in the WS-IS paradigm than in the oddball paradigm. It is therefore suggested that the stimulus-evaluation process for target stimuli in the WS-IS paradigm was quickly performed, resulting in the shortening of both P3b latency and EMG-RT.

In contrast, the amplitudes of P3b in the WS-IS paradigm did not differ from those in the oddball paradigm. This is consistent with the findings of Donchin et al. (Donchin et al., 1975; 1979), who showed that the amplitude of P300 was not affected by a warning stimulus. Johnson (1986; Johnson, 1988a) suggested that the amplitude of P300 was influenced by both stimulus complexity and task complexity (see Section 4.2.4), which are thought to be crucial factors for 'stimulus meaning.' Accordingly, in the oddball and WS-IS paradigms of this experiment, both the task complexity and stimulus complexity may be equivalent, suggesting that the stimulus meaning of the target stimuli in the WS-IS paradigm did not differ from that in the oddball paradigm.

Collectively, the results of N140 indicate that the target stimuli presented in both oddball and WS-IS paradigms may be processed with equivalent attentional (arousal) levels of the subjects, whereas, on the basis of P300 results, the target stimuli may be processed faster in the WS-IS paradigm than in the oddball paradigm. This implies that the WS reduces the necessary length of time spent in stimulus-evaluation system for the target stimuli.

The point of issue on SSR in the present experiment was whether or not the warning stimulus (WS) affects the elicitation of SSR. The results showed that the SSR evoked by target stimuli in the WS-IS paradigm did not differ from that in the oddball paradigm. This suggests that the presence of WS did not affect the elicitation of SSR. The results of SSR can be explained in terms of the following factors relating to the target stimuli: the attention (or arousal state) of the subjects, stimulus anticipation of the subjects, the meaning of the target stimulus, and the direct effects of motor commands.

The present results of N140 amplitudes indicated that subjects were equally attentive to the given stimuli in both the WS-IS and oddball paradigms. The reason why the SSR became equivalent in both the WS-IS and oddball paradigms in the present experiment may be that the attentional level (or arousal state) of the subjects was equivalent between the two paradigms. In other words, the presentation of WS may not influence the attentional level (arousal state) as a 'preparatory status' of the subjects in
producing voluntary movements.

For the stimulus-anticipation factor, the subjects seemed to be able to anticipate to some degree the appearance of imperative target stimuli and made preparations for motor response. This can be seen in the present results of shortening of both the P3b latency and EMG-RT in the WS-IS paradigm, which indicate that the time needed for both the stimulus evaluation and preparatory processes for motor response was shortened. However, SSR and R-R intervals prior to target stimulus in the WS-IS paradigm did not differ from those in the oddball paradigm. This suggests that the stimulus anticipation of subjects for WS presentation may affect both stimulus evaluation and movement-related processes but not the elicitation of SSR.

The third likely factor inherent in the target stimuli in the present experiment is the 'stimulus meaning' of the target stimulus (Johnson, 1986; Johnson, 1988a). The results of P3b amplitude indicate that the stimulus meaning of the target stimuli in the WS-IS paradigm did not differ from that in the oddball paradigm. In both paradigms, the target stimuli involved the stimulus meaning of motor responses. The results of the previous experiment (Experiment 2) also suggested that the requirement of motor response enhanced the stimulus meaning, related to forcing the subjects to make a voluntary movement, and then activated the SSR. It is therefore suggested that the stimulus meaning factor in the WS-IS paradigm may influence the elicitation of SSR to the same degree as in the oddball paradigm.

The final likely factor of the target stimuli in the present experiment is the actual production of voluntary movements. This may directly influence the SSR. It has been suggested that the EDA (such as SSR, SPR, and SCR) is an indicator of cutaneous modifications, effectively improving tactile acuity which enables fine motor control of the hands (Darrow, 1937; Gatchel & Lang, 1973). Sequeira and Roy (1993) showed, in their study using cats, that the cortical motor commands evoked EDA as a somato-autonomic response through the pyramidal tract irrespective of the reticulospinal neurons. In the present experiment, the target stimuli required subjects to produce an identical motor response for both WS-IS and oddball paradigms. The motor commands descending directly to skeletal muscles to be activated (which were generated in the motor areas) should therefore be identical in the two paradigms. Given the notions of Sequeira and Roy (1993), activation of the motor areas which generate motor commands could directly evoke the SSR (as discussed in the Section 4.2.4).
In addition, it is suggested that the nature of stimulus novelty was not a primary characteristic of the target stimuli in either paradigm used in the present experiment. As mentioned in the previous sections (Sections 4.1.4 and 4.2.4), SSR was originally thought to be sensitive to the novelty nature of the stimulus and processed in the automatic mode of information processing. This should also result in the elicitation of P3a and novelty P3 (Miyakawa et al., 1992; Deguchi et al., 1996; Knight, 1996; Lagopoulos et al., 1998). In the present experiment, the target stimuli were presented for 20% of all stimuli in both oddball and WS-IS paradigms, whereas in the WS-IS paradigm the target stimuli were preceded by the WS. In the latter case, it was predicted that the novelty nature of the target stimuli was almost eliminated because the subjects were able to anticipate to some degree the timing of the presentation of target stimuli. In fact, there appeared neither P3a nor novelty P3. This suggests that the nature of stimulus novelty was not a primary characteristic of the target stimuli in either paradigm used in the present experiment. This is consistent with the results of the previous experiments (Experiments 1 and 2).

In conclusion, even when the WS was presented (it should accelerate the stimulus evaluation processes for the target stimulus) the SSR arose similarly to when the WS was not presented. This suggests that stimulus anticipation may not affect the elicitation of SSR. Rather, both the attentional level (or arousal state) of subjects and the meaning of the target stimulus relating to motor production, which appeared equivalent for both the WS-IS and oddball paradigms, may affect the elicitation of SSR. In other words, the elicitation of SSR during voluntary movements is affected by movement-related processes (e.g., motor production) rather than the stimulus evaluation process. Moreover, motor production directly controlled by the movement-related cortical activities (e.g., activities in the primary motor area) may probably be important for the elicitation of SSR.
4.4  EFFECTS OF MOTOR PRODUCTION AND INHIBITORY AVOIDANCE ON SYMPATHETIC SKIN RESPONSE UNDER DIFFERENT VOLUNTARY OUTPUT CONDITIONS (EXPERIMENT 4)

4.4.1 INTRODUCTION

The results of Experiment 3 suggested that the elicitation of SSR during voluntary movement was affected by movement-related processes (i.e., response selection, response programming, and response execution), rather than stimulus evaluation processes (i.e., stimulus identification, decision-making, and context updating).

Movement-related processes should be mediated by the activation of cortical areas responsible for motor production (e.g., the primary motor area, supplementary motor area, and cingulate cortex). In the stage of response selection, subjects should make a decision to move when they detect a target signal/stimulus (i.e., Go stimulus) during reaction-time tasks. This is the motor production process. In contrast, when they detect a non-target signal/stimulus (i.e., NoGo stimulus), they should decide to avoid execution of the required movement. This is the motor inhibition process. Moreover, when subjects were presented with a WS prior to the following IS, they should prepare the required movement prior to IS. Nevertheless, when the IS is a non-target stimulus they should make efforts to avoid the release of the ‘prepared’ motor program and thus stop the execution of the ‘pre-programmed’ movements. In such WS-IS conditions, it is plausible that the Go and NoGo signal/stimuli as ISs evoke two different types of P300 component (i.e., Go- and NoGo-P300), respectively. In fact, the results of previous studies (e.g., Pfefferbaum et al., 1984; 1985; Roberts et al., 1994) indicated that the P300 components differed in both latency and scalp topography, suggesting that motor inhibition processes were functionally different from the motor production processes. It is still unclear whether or not the motor inhibition processes affect SSR during reaction-time tasks. In the present experiment, these movement-related processes (i.e., motor production and inhibition/avoidance processes) were examined in terms of ERPs and SSR.

The present experiment used a Go/NoGo paradigm with presentation of WS; three seconds after the presentation of WS, either a Go or NoGo stimulus was presented to the subjects with equivalent probability (i.e., 50 % vs. 50 %). The Go stimulus required the subjects to produce a motor response; thus, it invoked the motor production process. The
other NoGo stimulus required the subjects to inhibit the response; it invoked the motor inhibition process. It was therefore predicted that in the present experiment the Go stimuli would evoke a positive potential (Go-P300) and the NoGo stimuli a distinct positive potential (NoGo-P300) (for more details, see Section 3.1.4).

4.4.2 METHODS

4.4.2.1 Subjects

Ten neurologically normal volunteers (eight males and four females) aged from 20 to 28 years participated in the present experiment. Informed consent was obtained from each participant. The maximal voluntary contraction (MVC) of each subject, by extending the right elbow joint, was measured prior to the experiment. The experimental settings were as mentioned in Section 3.3.1.

4.4.2.2 Recordings of EEG, EMG, and SSR

The recordings of EEG, EMG, and SSR were the same as those used in Experiment 2.

An auditory click tone (60 dB, 1 msec duration) was generated as a warning signal (WS) using an auditory stimulator and delivered to the subjects via headphones. Force, which was produced by any movement of a subject’s right forearm, was monitored using an oscilloscope. The force was represented as a baseline in the window of the oscilloscope; when the subjects extend their right elbow joint, the baseline rose.

4.4.2.3 Procedures

The Go/NoGo paradigm consisted of combination of both auditory (WS) and electrical stimuli. In one trial, 3 sec after the WS presentation an electrical stimulus was randomly delivered to either the index (Go, 50 %) or the little (NoGo, 50 %) finger. The intertrial interval was 6-10 sec. The subjects were instructed to press down on the upper plate as fast as possible only when they detected the Go stimulus, and to fit the baseline to a fixed target line as accurately as possible (the target line was shown in the window of the oscilloscope). The subjects were also asked not to respond when they detected the NoGo stimuli.

After a 10-minute resting period, the Go/NoGo paradigm was performed under two conditions. In one condition (MVC20 condition), the target line was settled at 20 % of
the MVC measured prior to the experiment for each subject. For the other condition (MVC40 condition), the target line was settled at 40% of MVC. Each subject performed more than 40 trials in each condition. These two conditions were performed in an order counterbalanced between subjects.

4.4.2.4 Analyses of N140, P300, and SSR

The measurements of ERP and SSR were almost the same as those used in Experiment 2. EEG data converted into digital data were averaged over 16 samples for both Go and NoGo stimuli. SSR data were averaged over 16 samples with both Go and NoGo stimuli.

4.4.2.5 Statistics

Three-way ANOVAs were performed on the amplitude and latency of N140 and P300 for the following repeated-measures factors: conditions (C; MVC20 and MVC40), stimuli (S; Go and NoGo) and electrodes (E; F3, Fz, F4, C3, Cz, C4, P3, Pz and P4). Two-way ANOVAs were performed on the amplitude of SSR for the following repeated-measures factors: conditions (C) and stimuli (S).

In addition, difference waveforms of ERP were calculated by subtracting the waveform obtained for the Go stimulus from that for NoGo stimulus.

4.4.3 RESULTS

Figure 11 and Figure 12 show typical recordings of both ERP and SSR under the two conditions in one subject. In both MVC20 and MVC40 conditions, obvious P300 deflections appeared to both the Go and NoGo stimuli (Figure 11) but SSR was evoked by the Go stimuli, rather than by the NoGo stimuli (Figure 12).

4.4.3.1 N140 components

For the amplitudes of N140 (Table 18), neither the main effects nor the interactions of each factor were significant.

For the latencies of N140 (Table 19), the main effect of electrodes was significant (F=7.006, P<0.001). Contrast tests were then calculated among electrode sites. The results were as follows: i) at both central and parietal sites the N140 latencies at the left hemisphere (i.e., C3 and P3) were significantly shorter than those at the right hemisphere (i.e., C4 and P4; C3 vs. C4, P<0.01, P3 vs. P4, P<0.05); ii) at midline sites the N140
latencies were shorter at Cz than at Fz (P<0.01); and iii) at the left sites the N140 latencies at C3 and P3 were significantly shorter than those at F3 (C3 vs. F3, P<0.01, P3 vs. F3, P<0.05).

4.4.3.2 P300 components

For the amplitudes of P300 (Table 20), the main effect for stimuli was significant but also had significant interaction with electrode sites (F=14.307, P<0.001). The simple main effects for electrode sites were significant both for Go (F=29.014, P<0.001) and NoGo stimuli (F=16.283, P<0.001, Figure 13). Contrast tests were then calculated among the electrode sites for both stimuli. For Go stimuli, at the left, midline, and right sites the P300 amplitudes were largest at parietal sites among the frontal and central sites, except for at C4 (left, F3 vs. C3, P<0.001, F3 vs. P3, P<0.001, C3 vs. P3, P<0.05; midline, Fz vs. Cz, P<0.001, Fz vs. Pz, P<0.01, Cz vs. Pz, P<0.05; right, F4 vs. C4, P<0.001, F4 vs. P4, P<0.001). There were no lateral differences in the P300 amplitudes for the Go stimuli. For NoGo stimuli, the P300 amplitudes at Cz were largest among those at both the midline (Cz vs. Fz, P<0.001, Cz vs. Pz, P<0.01) and the central sites (Cz vs. C3, P<0.001, Cz vs. C4, P<0.001).

For the latencies of P300 (Table 21), the main effect of stimuli was significant (F=16.168, P<0.01), with the P300 amplitudes for Go stimuli being shorter than those for NoGo stimuli (Figure 14).

4.4.3.3 Difference waves

Difference waveforms (Figure 15) showed slight shifts toward negative potentials (negative shifts) in latency of 200-300 msec for both MVC20 and MVC40 conditions. The negative shifts tended to increase in the MVC40 condition compared with those in the MVC20 condition.

4.4.3.4 SSR

For the SSR (Figure 12), the main effect for stimuli was significant (F=11.967, P<0.01, Table 22) with the SSR was larger for Go stimuli than for NoGo stimuli.
Figure 11: Typical recordings of ERPs for the NoGo and Go stimuli in MVC20 and MVC40 conditions.
Figure 12: Typical recordings of SSRs for the NoGo and Go stimuli in MVC20 and MVC40 conditions.
Chapter 4 Experiments

Table 18: Amplitudes of N140 (μV) for the NoGo and Go stimuli in MVC20 and MVC40 conditions.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>NoGo Mean</th>
<th>NoGo SD</th>
<th>Go Mean</th>
<th>Go SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>MVC20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F3</td>
<td>-3.259</td>
<td>5.016</td>
<td>-2.931</td>
<td>5.012</td>
</tr>
<tr>
<td>Fz</td>
<td>-4.876</td>
<td>5.424</td>
<td>-2.853</td>
<td>4.193</td>
</tr>
<tr>
<td>F4</td>
<td>-4.957</td>
<td>4.956</td>
<td>-4.327</td>
<td>3.660</td>
</tr>
<tr>
<td>C3</td>
<td>-3.033</td>
<td>5.142</td>
<td>-2.962</td>
<td>5.019</td>
</tr>
<tr>
<td>Cz</td>
<td>-4.321</td>
<td>6.740</td>
<td>-4.687</td>
<td>5.902</td>
</tr>
<tr>
<td>C4</td>
<td>-4.375</td>
<td>4.224</td>
<td>-5.109</td>
<td>3.472</td>
</tr>
<tr>
<td>P3</td>
<td>-2.330</td>
<td>5.157</td>
<td>-2.668</td>
<td>4.804</td>
</tr>
<tr>
<td>Pz</td>
<td>-2.201</td>
<td>5.469</td>
<td>-2.863</td>
<td>4.939</td>
</tr>
<tr>
<td>P4</td>
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<td>-3.012</td>
<td>4.011</td>
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<td>MVC40</td>
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<td></td>
<td></td>
</tr>
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<td>Fz</td>
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<td>F4</td>
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<td>-5.158</td>
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<td>3.674</td>
<td>-2.792</td>
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<td>Cz</td>
<td>-6.597</td>
<td>4.986</td>
<td>-5.101</td>
<td>6.197</td>
</tr>
<tr>
<td>C4</td>
<td>-6.389</td>
<td>2.550</td>
<td>-5.051</td>
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<td>P3</td>
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<td>Pz</td>
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<td>5.101</td>
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<td>P4</td>
<td>-3.581</td>
<td>3.327</td>
<td>-3.181</td>
<td>3.931</td>
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Table 19: Latencies of N140 (msec) for the NoGo and Go stimuli in MVC20 and MVC40 conditions. 
Note gives a summary of the ANOVAs for a significant main effect for electrodes (E) on the N140 latencies.

<table>
<thead>
<tr>
<th>Electrode sites</th>
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<th>Go</th>
</tr>
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<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
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<td>MVC20</td>
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<td>Cz</td>
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<td>Pz</td>
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<tr>
<td>P4</td>
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<td>20.843</td>
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<tr>
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<td>F3</td>
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<td>Fz</td>
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<td>20.575</td>
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<tr>
<td>P4</td>
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<td>15.102</td>
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Note: F=7.006, P<0.001, for Electrodes
Table 20: Amplitudes of P300 (μV) for the NoGo and Go stimuli in MVC20 and MVC40 conditions.

Note gives a summary of the ANOVAs for a significant interaction between stimuli and electrodes (S*E) on the P300 amplitudes.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>NoGo Mean</th>
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<th>Go Mean</th>
<th>Go SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>MVC20</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>F3</td>
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<td>7.021</td>
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<td>3.663</td>
</tr>
<tr>
<td>Fz</td>
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<td>6.215</td>
<td>11.992</td>
<td>4.616</td>
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<td>F4</td>
<td>17.923</td>
<td>6.453</td>
<td>12.546</td>
<td>5.173</td>
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<tr>
<td>C3</td>
<td>19.549</td>
<td>5.352</td>
<td>16.830</td>
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<tr>
<td>Cz</td>
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<td>8.081</td>
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<td>5.905</td>
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<td>2.791</td>
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<td>5.186</td>
<td>18.017</td>
<td>4.641</td>
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</table>

Note: F=14.307, P<0.001, between Stimuli and Electrodes
Figure 13: Mean P300 amplitudes for each stimulus (NoGo and Go) in MVC20 and MVC40 conditions as a function of coronal electrode site for the frontal, central, and parietal electrode positions.
Table 21: Latencies of P300 (msec) for the NoGo and Go stimuli in MVC20 and MVC40 conditions. Note gives a summary of the ANOVAs for a significant main effect for stimuli (S) on the P300 latencies.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>NoGo Mean</th>
<th>SD</th>
<th>Go Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>MVC20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F3</td>
<td>313.0</td>
<td>32.506</td>
<td>269.0</td>
<td>28.752</td>
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<tr>
<td>Fz</td>
<td>317.0</td>
<td>36.148</td>
<td>276.5</td>
<td>37.642</td>
</tr>
<tr>
<td>F4</td>
<td>315.5</td>
<td>36.013</td>
<td>274.5</td>
<td>35.233</td>
</tr>
<tr>
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<td>28.911</td>
<td>271.5</td>
<td>26.463</td>
</tr>
<tr>
<td>Cz</td>
<td>308.5</td>
<td>30.373</td>
<td>269.0</td>
<td>29.326</td>
</tr>
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<td>313.5</td>
<td>31.539</td>
<td>282.0</td>
<td>32.249</td>
</tr>
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<td>278.5</td>
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<td>Pz</td>
<td>310.5</td>
<td>30.500</td>
<td>278.5</td>
<td>28.387</td>
</tr>
<tr>
<td>P4</td>
<td>318.0</td>
<td>28.008</td>
<td>280.0</td>
<td>29.250</td>
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<td>315.5</td>
<td>26.505</td>
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</tr>
<tr>
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<td>270.0</td>
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<td>309.5</td>
<td>24.659</td>
<td>275.0</td>
<td>39.511</td>
</tr>
<tr>
<td>Cz</td>
<td>309.5</td>
<td>25.761</td>
<td>267.5</td>
<td>37.657</td>
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<td>24.585</td>
<td>271.5</td>
<td>31.890</td>
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<tr>
<td>P3</td>
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<td>30.732</td>
<td>284.0</td>
<td>38.137</td>
</tr>
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<td>Pz</td>
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<td>34.721</td>
<td>284.0</td>
<td>38.137</td>
</tr>
<tr>
<td>P4</td>
<td>318.0</td>
<td>32.846</td>
<td>286.0</td>
<td>42.869</td>
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</table>

Note: F=16.168, P<0.01, for Stimuli
Figure 14: Mean P300 latencies for each stimulus (NoGo and Go) in MVC20 and MVC40 conditions as a function of coronal electrode site for the frontal, central, and parietal electrode positions.
Figure 15: Difference waveforms of ERP ([NoGo – Go], grand average) in MVC20 and MVC40 conditions.

ERPs; Difference waves

- MVC20
- MVC40
Table 22: SSR amplitudes (mV) for the NoGo and Go stimuli in MVC20 and MVC40 conditions.  
Note gives a summary of the ANOVAs for a significant main effect for stimuli (S) on the SSR amplitudes.

<table>
<thead>
<tr>
<th>Conditions</th>
<th>NoGo Mean</th>
<th>NoGo SD</th>
<th>Go Mean</th>
<th>Go SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>MVC20</td>
<td>0.356</td>
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<td>MVC40</td>
<td>0.407</td>
<td>0.375</td>
<td>3.393</td>
<td>2.625</td>
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</table>

Note: F=11.967, P<0.01, for Stimuli
4.4.4 DISCUSSION

The purpose of this experiment was to examine the effectiveness of the motor production and inhibition processes on elicitation of SSR. The results of ERPs will be first discussed on the basis of the processes that should be related to response selection and response execution/suppression. Following this, the effects of both motor production and inhibition processes on elicitation of SSR will be discussed.

In both MVC20 and MVC40 conditions, N140 components were clearly evoked by both Go and NoGo stimuli in each condition. The obvious N140 components reflected that the subjects were much more attentive to the given stimuli (see Sections 4.1.4, 4.2.4, and 4.3.4). In the present experiment, subjects were asked to respond to Go stimuli and to stop the motor responses to NoGo stimuli, they thus had to discriminate between these two stimuli. It is therefore suggested that in both conditions the attentional level of the subjects was enhanced in order to discriminate between the Go and NoGo stimuli.

The amplitudes of the P300 for Go stimuli (Go-P300) did not differ from those for the NoGo stimuli (NoGo-P300). The latencies of the both P300s were longer than that of the so-called P3a (or novelty P3, see Section 2.2.2.2.1). These results indicate that both the Go and NoGo stimuli may be processed with equivalent attentional (or processing) resources of the subject, and that not only the Go stimuli but also the NoGo stimuli may be processed in the controlled mode of information processing of the brain (see Section 4.1.4).

After completion of the present experiments, the participants reported that it was difficult to match the baseline to the target line during each condition (e.g., pressing a plate with extension of the elbow joint). Johnson (1988a) has suggested that increasing task complexity with motor response tasks enhance the P300 amplitudes. In the present results, the amplitude of P300 did not differ between the MVC20 and MVC40 conditions. Therefore, it is suggested that during both conditions the task complexity might have equally affected the P300 amplitudes (see Section 4.2.4).

Between the MVC20 and MVC40 conditions, there should be a difference in motor programs serving motor responses, because the to-be-required motor responses in each condition were different from each other in terms of the muscular output for movements. It was thus speculated that the difference in motor programs might affect the P300 and SSR. However, the results of both P300 and SSR showed no difference between MVC20 and MVC40 conditions. This speculation was therefore disproved.
Both the latencies and scalp distributions of the Go-P300 were different from those of the NoGo-P300. The latencies of NoGo-P300 were longer than those of Go-P300. The amplitude of NoGo-P300 was largest at the central electrode sites (Cz) in contrast to that of Go-P300 being largest at the parietal among all of the electrode sites. In a Go/NoGo paradigm, Pfefferbaum et al. (1984; Pfefferbaum et al., 1985) showed that Go and NoGo stimuli evoked parietal maximum P3b (Go-P300) and centro-parietal maximum P300-like component (NoGo-P300), respectively. They also reported that the latency of NoGo-P300 was longer than that of Go-P300. Pfefferbaum et al. suggested that the NoGo-P300 reflected the motor inhibition process, while the Go-P300 reflected the motor production processes. The present results of P300s were consistent with the results of Pfefferbaum et al. Associations of positive slow potentials (i.e., NoGo-P300) with the interruption of motor production processes (Roberts et al., 1994) or the disfacilitation of neuronal networks for response execution (Schupp et al., 1994) have also been proposed. It is therefore suggested that the NoGo-P300s appearing in the present experiment might be related to the motor inhibition processes.

The difference waveforms of ERPs in each MVC condition (which calculated by subtracting the waveform obtained for Go trial from that for NoGo trial) showed negative shifts in latency with a range of 200 to 300 msec at most electrode sites. The negative shifts seemed to be larger in the MVC40 condition (in which the subjects would make much greater efforts to stop their motor response) than in the MVC20 condition. It was reported that the N2 component appeared when subjects decided to stop the response movements (Simson et al., 1977, see Section 2.2.2.4; Pfefferbaum et al., 1985; Gemba & Sasaki, 1989; Jodo & Kayama, 1992). Some researchers have suggested that decision-making (i.e., deciding to move or stop) is provided by activation of the premotor area (PMA, Wise et al., 1983; Mitz et al., 1991; di Pelligrino & Wise, 1993; Kalaska & Crammond, 1995) in the prefrontal cortex and anterior cingulate cortex (Devinski et al., 1995). Especially, the activity of the PMA was supposed to evoke the N2 component of ERPs under the NoGo situation (Jodo & Kayama, 1992; Sasaki et al., 1993). Jodo and Kayama (1992) indicated that the amplitude of N2 was enhanced when subjects were required to make more efforts to stop the 'pre-programmed' motor response. These characteristics of the N2 component seem to be similar to those of the negative shifts that appeared in the present results. It is therefore suggested that the motor inhibition process may occur with activation of the PMA during NoGo trials.
Collectively, both Go and NoGo stimuli might be processed in the controlled mode of information processing with equivalent attentional resources of subjects. Task complexity, which affects the P300 amplitude, is thought to be equivalent during both the MVC20 and MVC40 conditions. Go- and NoGo-P300 may reflect the motor production and motor inhibition processes, respectively. In addition, the NoGo stimuli in the MVC40 condition required the subjects to make much more effort to inhibit 'pre-programmed' movements than in the MVC20 condition.

In the present results, it was shown that large SSR appeared when Go stimuli were presented but not when the NoGo stimuli were presented. According to the results of ERPs, both Go and NoGo stimuli might be processed in the controlled mode of information processing of the brain. Also, the task complexity of the motor response might affect the P300 amplitude during both MVC20 and MVC40 conditions. The previous results of this chapter (Experiments 1, 2, and 3) suggested that the SSR was mediated by the motor production processes in which the SSR-eliciting stimuli were processed in the movement-related, controlled mode of information processing. This means that the activity of the movement-related brain areas (i.e., MI, SMA, and anterior cingulate cortex) might affect the elicitation of SSR. In the present experiment the Go stimuli required subjects to produce voluntary movements, as with the target stimuli used in the previous experiments of this chapter (Experiments 1, 2, and 3). In addition, the scalp distributions of Go-P300 were similar to the P3b evoked by the target stimuli in the previous experiments. These indicate that the Go stimuli may be processed in the controlled mode as well as the target stimuli. It is therefore supported that the motor production processes (i.e., response selection and following execution of voluntary movements) and the activity of the movement-related brain areas are related to the elicitation of SSR.

For the NoGo trials, the SSR waves were significantly smaller than those in Go trials. According to the results of ERPs, NoGo stimuli were processed in the controlled mode with attentional resources of subjects required to process them, as well as the Go stimuli. These may indicate that the stimulus evaluation processes reflected by P300 measurements do not affect the elicitation of SSR. Rather, it is possible that the movement-related processes, especially motor production or inhibition processes, should affect the SSR elicitation.

The main difference between motor production and motor inhibition processes is whether or not the primary motor area (MI) generates the motor command. Some
researchers (Sequeira & Roy, 1993, see Section 2.3.4; Devinski et al., 1995; Fredrikson et al., 1998) have suggested that the motor commands generated by activation of MI, which accompanies activation of the supplementary motor area and the anterior cingulate cortex, invoke the EDA (EDA, such as SSR, SCR, SPR). Sequeira and Roy (1993) indicated that the SPR appeared when the motor commands descend to the skeletal muscles through the pyramidal tract (Sequeira and Roy called this the ‘pyramidal control of EDA’). The pyramidal control of EDA is suggested to directly affect the EDA, being independent from the ARAS activation. During the NoGo trials in the present experiment the MI might not activate with the presentation of NoGo stimuli, and it is therefore possible that SSR merely appears when the subjects do not perform a motor response.

It is also suggested that activities of the brain areas relating to motor inhibition processes may diminish the SSR. Schupp et al. (1994) showed that amplitude of the eyeblink reflex, which reflects excitability of the midbrain and brainstem, decreased during NoGo situations. They indicated that a fronto-central P300-like positivity evoked by NoGo stimuli, which required ‘active inhibition of the pre-programmed motor responses,’ could be seen as a sign of the activation of the prefrontal cortex. They also supposed that such inhibition of pre-programmed responses (i.e., cortico-fugal disfacilitation) by activation of the prefrontal cortex was the main reason for the decrement in amplitude of eyeblink reflex. Cechetto and Saper (1990) pointed that the frontal lobes, particularly the orbital, insular and prefrontal cortex, had a predominant influence on the control of autonomic responses. In the present experiment, the NoGo-P300 showed a central maximum distribution, resembling the P300-like positivity which appeared in the results of Schupp et al. According to the results of ERPs, the NoGo-P300 and the negative shifts would reflect neural activities in the prefrontal brain regions (such as the PMA, Jodo & Kayama, 1992) relating to motor inhibition. It is therefore suggested that the elicitation of SSR may be suppressed by the activity of the prefrontal cortex (including the PMA) relating to motor inhibition processes.

In conclusion, it is suggested that the elicitation of SSR is mediated by movement-related processes. Particularly, SSR may well be enhanced when subjects actually perform voluntary movements. It is also likely that the SSR may be suppressed when subjects have to stop the execution of prepared movements. These may not be affected by the difference between two types of response movements (i.e., MVC20 and MVC40) in this experiment.
CHAPTER 5 SUMMARY AND CONCLUSIONS

Recent studies on the elicitation of SSR (e.g., Shahani et al., 1984; Knezevic & Bajada, 1985; Baba et al., 1988; Elie & Guiheneuc, 1990; Arunodaya & Taly, 1995) have suggested that SSR arises when the given stimuli are either novel, startling, or unpredictable for subjects. It has been demonstrated that such characteristics of the stimuli (i.e., novel, startling, unpredictable stimuli) are responsible for the appearance of the P3a component of ERPs on the human scalp. Miyakawa et al. (1992) showed that both the SSR and the P3a component of ERPs appeared concurrently in a non-attention-demanding task, suggesting that the SSR was a manifestation of the orienting response of the autonomic nervous system. Deguchi et al. (1996) also showed that infrequently given, novel stimuli evoked the SSR with the appearance of the novelty P3. In contrast, Knight (1996) showed that both the novelty P3 and SSR were impaired in patients with hippocampal lesions as compared with neurologically normal subjects. The hippocampus is related to the detection of novelty nature of stimuli. Both the novelty P3 and P3a were therefore thought to appear when the given stimulus was processed in the non-attention-demanding, automatic mode of information processing in the brain (Table 23-B). Accordingly, the results of these previous studies suggested that the SSR was an index of orienting response of the autonomic nervous system; the orienting response which was mediated by automatic processing of the given stimuli.

Table 23: Explanations for each parameter of the ERP components used in this study (A), and the processing mode reflected in two subcomponents of P300 (B). For details, see also Chapter 2.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Explanations</th>
</tr>
</thead>
<tbody>
<tr>
<td>N140</td>
<td>amplitude</td>
</tr>
<tr>
<td>P300</td>
<td>amplitude</td>
</tr>
<tr>
<td></td>
<td>latency</td>
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<table>
<thead>
<tr>
<th>Subcomponents</th>
<th>Processing modes in the brain</th>
</tr>
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<tbody>
<tr>
<td>P3a/novelty P3</td>
<td>Non-attention-demanding, automatic mode</td>
</tr>
<tr>
<td>P3b</td>
<td>Attention-demanding, controlled mode</td>
</tr>
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</table>
In contrast, Osada et al. (1998a) showed an enhancement of SSR in a reaction-time task in which subjects were required to concentrate their attention on given stimuli. This suggests that the SSR could also appear when the given stimuli are processed in attention-demanding, controlled mode, rather than the automatic. The attention-demanding, controlled mode of information processing is largely mediated by arousal or conscious awareness. It is well known that as the level of arousal or conscious awareness of subjects becomes lower, the electrodermal activities (EDA) such as skin conductance (SCR), skin potential responses (SPR), and SSR often decrease (Bloch et al., 1965). Elie and Guiheneuc (1990) also showed an alleviation of SSR amplitudes with habituation occurring in long-term experiments. These findings suggest that the SSR may be mediated by the attention and/or arousal level of subjects. Furthermore, Aihara et al. (1998) have recently suggested that the habituation appearing in SSR is less during the preparation of mental and motor activities. Such characteristics of the SSR habituation may probably depend on the 'excitability level' of the sympathetic neuron pool which is controlled by the ascending reticular activating system (ARAS). Since the ARAS is thought to be activated by cortical excitation, it is possible that the functions of higher brain centers (such as the motor areas) mediate the elicitation of SSR (e.g., Sequeira & Roy, 1993). In this regard, it is worthy to examine whether the sympathetic nerve activity such as SSR is activated with the execution of voluntary movements (e.g., Siddle et al., 1979).

Experiment 1 examined which mode of information processing, automatic or controlled, is more effective in evoking SSR during reaction-time tasks. In the experiment, frequent-standard, infrequent-nontarget, and infrequent-target stimuli were randomly presented to subjects under both the attend condition (i.e., the subjects were asked to perform a voluntary movement responding to the infrequent-target stimuli) and the ignore condition (i.e., the subjects were instructed to ignore all of the stimuli). An oddball paradigm using these three types of stimuli was employed to examine differences between the novel (i.e., infrequent) and task-relevant (i.e., target) nature of the given stimulus. The novel nature of stimuli is thought to be a primary causal factor for the elicitation of novelty P3 and/or P3a, while the task-relevant nature of stimuli may be responsible for the elicitation of P3b.

The results of Experiment 1 showed that in the attend condition SSR apparently appeared with the target stimuli alone, but not with either nontarget or standard stimuli. However, in the ignore condition SSR did not clearly appear with either nontarget or target...
stimuli. In the attentive condition alone, P3b appeared for the target stimuli, while positive potentials like P3b appeared for the nontarget stimuli with latencies longer than those of P3b. This indicated that two types of infrequent stimuli (i.e., target and nontarget) in the attentive condition are processed in the controlled, attention-demanding mode of information processing, because P3b is an index of attention-demanding processing (Table 23-B). The amplitudes of the N140 component of ERPs appeared larger in the attend condition than in the ignore condition. This also indicated that the attentional level (or arousal state) of the subjects was increased in the attend condition (Table 23-A). These results of both SSR and ERPs therefore suggest that the target stimuli in the attentive condition are processed in the attention-demanding, controlled mode of information processing and that SSR appears when the given stimuli are processed in the controlled, rather than the automatic, mode of information processing.

In Experiment 1, the target stimulus was used to require the subjects to produce a motor response as well as to detect the given stimulus. This means that the stimulus was characterized by two types of task relevant meaning (i.e., target detection and motor production). Therefore, the results of Experiment 1 raised the further issue of which meaning, the detection of target stimulus or the production of voluntary movement, is effective in evoking SSR. Psychophysiological studies on EDA suggested that SCR was enhanced when subjects were asked to perform a voluntary movement as the desired motor response to a given stimuli. For example, Siddle et al. (1979) reported that subjects who were asked to perform a quick reaction-time response showed larger SCRs than those of subjects not asked to do so. Siddle et al. suggested that the EDA responses are enlarged when subjects make motor responses and that some motor-related nature of the given stimulus requiring the subjects to perform a desired motor response may affect the EDA responses. Although the Siddle et al. study did not report any empirical data indicating activities of the central nervous system, their suggestion seems quite plausible and should therefore be further examined.

Experiment 2 then examined the effectiveness of two types of task-relevant nature of the stimuli, that is, the target detection and motor production, on the elicitation of SSR using oddball paradigms. Subjects were asked to count in mind the number of presentations of infrequent target stimulus. This was concerned with the target detection nature (count condition). In the other condition, they were asked to respond to the target stimulus as quickly as possible by performing a voluntary movement (reaction condition).
The results showed that the amplitudes of SSR appeared larger in the reaction condition than in the count condition. N140 (an indicator of the activation level of subjects' attention, Table 23-A) was also larger in amplitude for the reaction condition than for the count condition, indicating that the attentional level (arousal state) of the subjects was higher in the reaction condition than in the count condition. In contrast, P300 (P3b, indicating attentional resources of subjects, Table 23-A) did not differ between these two conditions, indicating that the target stimuli presented in both the reaction and count conditions may be processed with similar levels of attentional resources. Accordingly, the increment of SSR in the reaction condition is probably not affected by the allocation of attentional resources (i.e., reflected in P3b) of the subjects. In contrast, the requirement of a quick motor response in the reaction condition may characterize the target stimulus with a specific stimulus meaning differing from that (i.e., target detection) in the count condition. This may have resulted in the SSR increment as well as the N140 amplitude in the reaction condition. It is therefore suggested that the target stimulus used for requiring motor production may enhance both the arousal state (attentional level) of subjects and the stimulus meaning which forces the subjects to perform a desired movement rather than simple counting. Both the enhanced arousal state and stimulus meaning may then activate the sympathetic nerve responses (i.e., SSR).

Motor production may further involve two types of information processing: the stimulus evaluation process (i.e., including the stimulus identification, decision-making, and context updating) and movement-related process (consisting of the response selection, response programming, and response execution). The former is reflected in ERPs, especially in the latency of P3b, which is thought to be a useful index of processing time spent for stimulus evaluation (Table 23-B). For the movement-related processes, EMG-RT is usually used to evaluate the total time spent for the information processing of stimulus identification, response selection and programming, and the delivery of motor commands to the relevant skeletal muscles. Both the P3b latency and EMG-RT are well known to decrease in reaction-time tasks with a warning signal/stimulus (WS) given to subjects prior to the imperative signal/stimulus (IS). This can be explained in terms of both the anticipation of stimulus and preparation of voluntary movement during the WS-IS interval. Such a WS-IS paradigm has often been used when investigating the relationships between the autonomic and cortical activities taking place during WS-IS intervals (see Appendix A). These studies suggest that cortical excitation in both processes of the stimulus
anticipation and motor preparation may activate the ascending reticular activating system (ARAS). The activation of ARAS should result in some enhancement in SSR, because ARAS is thought to control the frequency of sympathetic discharge. However, it is still unclear whether or not the SSR evoked by the IS can be affected during a WS-IS reaction-time task.

In Experiment 3, the effectiveness of the presentation of WS on the elicitation of SSR evoked by the IS was examined in terms of comparisons between two different conditions; in one condition there was no WS (the typical oddball paradigm), while in the other condition WS was presented to subjects prior to IS (WS-IS condition). The results of Experiment 3 showed that the amplitudes of neither N140 nor P3b evoked by the IS differed between these two conditions, suggesting that neither the attention (or arousal level) of the subjects nor the stimulus meaning differed between the two conditions. The latencies of P3b and EMG-RT appeared shorter in the WS-IS condition than in the oddball condition. This indicated that the processing time spent for stimulus evaluation was shortened by the presentation of WS, which should evoke subjects' anticipation for the forthcoming stimulus (i.e., the IS). In contrast, the SSR did not differ between the two conditions, suggesting that both the anticipation of forthcoming stimulus and its evaluation process (reflected in P3b latency) may have no effect on SSR. Rather, the attention of the subjects and the meaning of the target (IS) stimulus (reflected in the amplitudes of P3b and N140) relating to motor production may evoke the SSR equally for the two conditions.

Movement-related processes (i.e., response selection, response programming, and response execution) should be mediated by the activation of cortical areas which are responsible for motor production (e.g., the primary motor area, supplementary motor area, and cingulate cortex). In the processing stage of response selection, subjects should make a decision to move (motor production process) when they perceive a target signal/stimulus (Go stimulus) during a reaction-time task. In contrast, when they perceive a non-target signal/stimulus (NoGo stimulus), they should decide to avoid execution of the required movement (motor inhibition processes). Moreover, when subjects are given a WS prior to the following IS, they should prepare prior to the IS the required movement ready to go. Nevertheless, when an IS is non-target they should make efforts to avoid the release of the 'prepared' motor program and thus stop the execution of 'pre-programmed' movements. In such WS-IS conditions, it is plausible that the Go and NoGo signal/stimulus as an IS should evoke two different types of P300 components (i.e., Go- and NoGo-P300).
respectively. In fact, the results of previous studies (Simson et al., 1977; Pfefferbaum et al., 1985) showed that the NoGo-P300 evoked by the IS (to which the subjects were asked to avoid the execution of pre-programmed movements) differed in both latency and the scalp topography compared with the Go-P300, suggesting that the motor inhibition processes were functionally different from the motor production processes.

In Experiment 4, the movement-related processes (i.e., motor production and inhibition/avoidance) were examined in terms of ERPs and SSR under the Go/NoGo paradigm. In addition, the effect on the elicitation of SSR of different movements as desired responses to target stimuli was examined. The results showed that the P3b (Go-P300) appeared when the subjects received the Go stimulus, whereas a P300-like potential (NoGo-P300), which was characterized by both longer latency and centro-parietal predominant amplitude compared with the Go-P300, appeared when the subjects received the NoGo stimulus. In the NoGo trials, a negative deflection in potential like the N2 component, which is thought to reflect a neural activity relating to motor inhibition (or avoidance), also appeared. This indicates that the subjects probably made efforts to avoid the execution of prepared movements. The SSR for the Go stimulus was significantly larger than that for the NoGo stimulus. These tendencies did not alter for the two types of response strength (i.e., 20% and 40% of maximal voluntary contraction of the brachial muscles). It was therefore suggested that the elicitation of SSR was mediated by movement-related processes irrespective of muscular strength. Specifically, SSR may well be enhanced when subjects actually perform a movement, while when subjects have to avoid the execution of a prepared movement (i.e., motor inhibition processes) the SSR may be suppressed.

On the basis of the findings of all the experiments conducted in this study, it is suggested that SSR appears with a given stimulus which requires subjects to perform actual voluntary movements, in which afferent inputs derived from the stimulus are processed by the brain in the movement-related, controlled mode of information processing. The elicitation of SSR during voluntary movements may be affected, at least, by either the attention-demanding processes, the meanings of stimuli, and/or cortical activities of movement-related brain areas (e.g., the primary and supplementary motor areas, and limbic cortex). Electrodermal activities (EDA), such as SSR, SCR, and SPR reflect the excitation level of the sympathetic nervous system and have been suggested to be controlled by the reticular formation and hypothalamo-limbic structures (see Chapter 2).
These brain areas are thought to perform important roles in generating the subjects' attention and evaluating the stimulus meaning. The results of this study are consistent with the notion that the mechanisms of the sympathetic nervous system are influenced by the activities of neocortical brain structures (such as the primary and supplementary motor area) which are crucial in preparing the motor program of desired voluntary movements. Sequeira and Roy (1993) precisely examined whether the motor cortex (i.e., the primary motor areas) could generate autonomic efferences together with the motor programs, showing that after a bulbar transection, in which all descending pathways except the pyramidal tracts were interrupted, stimulation of the motor cortex (area 4) still evoked SPR. The present study showed that the sympathetic activity is activated when subjects perform a voluntary movement, whereas it is inhibited when the subjects are required to avoid the execution of prepared voluntary movements (Experiment 4). This is also consistent with the findings of Sequeira and Roy. These findings emphasize an important role of motor commands descending to skeletal muscles for enhancing SSRs (i.e., sweat gland responses). However, there are of course some limitations in this study. The sympathetic nerve of the skin is known to innervate both the sweat glands and vessels in the skin (Hagbarth et al., 1972). These two components (i.e., sudomotor and vasomotor) are thought to work independently of each other (Arundodaya & Taly, 1995). Therefore, it is noted that the results of this study should be limited to the sudomotor component alone among skin sympathetic nerve activities.

Furthermore, this study was concerned with the activity of the sympathetic nervous system alone, although the autonomic nervous system consists of both sympathetic and parasympathetic nervous systems. Both nervous systems collaborate and play important roles in maintaining the 'homeostasis' of the human body. To closely elucidate the function of the autonomic nervous system during voluntary movements, the parasympathetic nervous system should also further be examined in the future.

In conclusion, it appears that the skin sympathetic nerve activity (i.e., SSR) may be generated by not only the non-attention-demanding, automatic mode of information processing in the brain, as traditionally suggested by a number of previous studies (e.g., Miyakawa et al., 1992; Deguchi et al., 1996; Knight, 1996), but also by the attention-demanding, movement-related, controlled mode of information processing, with the brain activities of the neocortical and the limbic structures. In this sense, this study clearly supports with empirical evidence the findings of Osada et al. (Aihara et al., 1998; Osada et
al., 1998a), Sequeira and Roy (1993), and Siddle et al. (1979), who suggest that SSR (and/or SPR) appears when the given stimuli are processed in the attention-demanding, movement-related, controlled mode of information-processing. This study further emphasizes the effectiveness on SSR elicitation of cortical (such as the frontal lobes, the primary and supplementary motor areas) activities relating to voluntary movements, which perform key roles for motor production as well as motor inhibition (or avoidance) processes. These factors may probably influence the skin sympathetic nerve activity. Furthermore, all the experiments described in Chapter 4 clearly demonstrated the utility of the dual recordings of ERPs and SSRs in examining the functions of cortical and sympathetic nerve activities as well as cortical-sympathetic functional relationships during human motor (and also mental) behaviors. In other words, simultaneous recordings of SSR and ERPs are a useful method to examine the integration of central and peripheral aspects relating to human voluntary movements.
APPENDIX A: CHANGES IN AUTONOMIC AND CORTICAL ACTIVITIES BEFORE THE ONSET OF VOLUNTARY MOVEMENTS

The relationship between the ANS and the CNS has been investigated by a number of researchers (Conner & Lang, 1969; Lacey & Lacey, 1970; Coles & Duncan-Johnson, 1975; Lacey & Lacey, 1978; Simons et al., 1979; Lacey & Lacey, 1980; Simons, 1988; Rockstroh et al., 1989; Rockstroh & Elbert, 1990; Otten et al., 1995; Koers et al., 1997). These researchers have used various indices of the autonomic (e.g., HR, blood pressure, electrodermal activities) and cortical neural activities (e.g., electroencephalogram, EEG, and event-related brain potentials, ERPs), especially HR and the contingent negative variation (CNV). The CNV, which is recorded on the scalp, appears during the interval between a signal (S1, or warning signal, which requires the subjects to attend the next signal) and the subsequent signal (S2, or imperative signal, which requires the subjects to perform voluntary movements). The subjects were asked to respond to the S2 with fast voluntary movements. Between the S1 and S2, the subjects have to anticipate the presentation of S2 (i.e., signal/stimulus anticipation), and prepare their voluntary movement responses to the S2 (i.e., motor preparation). It is suggested that the CNV reflects both the stimulus anticipation and motor preparation.

Lacey and Lacey (1970) first described the phenomenon of HR deceleration (decrement of HR) preceding the onset of voluntary movements. They reported that the HR deceleration started prior to a negative ERP shift and about 6 sec prior to the overt voluntary movements, suggesting that the HR "leads", or triggers, the negative ERP. Furthermore, Lacey and Lacey (1978) reported a time-dependent bradycardia (i.e., decrement of HR) for both subject- and experimenter-paced button presses.

Elbert et al. (1984) has confirmed that the onsets of HR deceleration and movement-related cortical potentials (i.e., the bereitschaftspotential, Kornhuber & Deecke, 1965) can concurrently occur. In their experimental paradigm, subjects were asked to press a button about twice a minute. This button press resulted in different consequences in two groups of subjects: for one group, the button press produced no external change in one block of trials but resulted in a 6-sec tone in another trial block. For the other group, the motor response started a reaction time trial with the imperative stimulus (IS) occurring after 6 sec; in one trial block, the IS was preceded by a warning stimulus (WS), whereas in
another trial block, this WS was absent. HR around a voluntary motor response showed a triphasic pattern comparable to the pattern observed in an experimenter-paced two-stimulus paradigm (WS-IS paradigm). The HR first decreased prior to the onset of the voluntary button-press movement. This is consistent with the findings of Lacey and Lacey (1970). However, HR was not invariably associated with the bereitschaftspotential, thus, HR deceleration was pronounced irrespective of whether the button press produced a tone or no external change. In contrast, the amplitude of bereitschaftspotential remained small under both conditions. However, when the button press initiated a reaction time trial, the bereitschaftspotential was pronounced, while the deceleration preceding the button press was truncated. Following the button press, a large slow negativity (i.e., contingent negative variation, CNV, Walter et al., 1964) and a pronounced second HR deceleration occurred in anticipation of the IS. Wölk et al. (1989) also demonstrated that both HR and blood pressure show triphasic changes with simultaneous development of CNV in a WS-IS paradigm.

A triphasic HR response is typically found under two stimulus conditions (e.g., WS-IS paradigm). A brief initial deceleration is followed by an accelerative component and by a second deceleration that reaches its nadir with the anticipated IS. While the response requirements and/or the relevance of the anticipated events have only small impact on the first deceleration, they strongly affect the subsequent components, suggesting dissociation between early and later portions of the cardiac response. Since they do not covary solely with motor requirements, Simons (1986) concluded that response requirements exert their effects by enhancing their significance or by directing more attention to IS. Simons et al. (1979), recording CNV, electrodermal response (i.e., skin conductance response, SCR), and HR with a WS-IS paradigm, have demonstrated that the presence of motor response requirements prompted anticipatory acceleration of the heart (i.e., increment of HR) and enhancement of both SCR and CNV. They considered that while the cortical responses (e.g., CNV) were very sensitive indicators of anticipated interest, visceral activity (e.g., HR and SCR) was seen to reflect a general mobilization of energy for efficient task performance. Parallels between HR decelerations and components of the CNV within the anticipation interval, as well as a similar sensitivity to experimental manipulations, suggest a functional relationship between the two event-related responses (ERRs, Rockstroh & Elbert, 1990). Thus, the early component of the CNV is coextensive with the first HR deceleration, and both responses can be elicited by single stimuli. The
correspondence between the terminal CNV and the second HR deceleration suggests that they may both reflect response preparation.

Moreover, Otten et al. (1995), recording CNV, P300 (evoked by significant warning signals), heart rate and blood pressure, confirmed a larger general responsiveness or emotional involvement during speed-maximizing trials. Recently, Fredrikson et al. (1998), using positron emission tomography (PET), suggested that electrodermal responses, such as SCR, skin potential response (SPR), and sympathetic skin response (SSR), seemed to reflect movement-related processes which are cognitively or emotionally mediated. According to these studies, it is suggested that preparatory changes in the autonomic responses are cognitively or emotionally mediated by preliminary instruction of the requirement for motor response.

It has also been reported that electrodermal activity (Yamazaki, 1977) and skin sympathetic nerve activity (Saito & Mano, 1992) increased prior to motor responses during the WS-IS interval (foreperiod). Yamazaki (1977) reported that CNV developed during a 6-sec foreperiod and SPR appeared following motor and psychological response. From these results, it was suggested that 1) the CNV and the SPR were generated from adjacent structures, 2) tonic and phasic autonomic changes occur during the CNV paradigm, and 3) a psychological process during the foreperiod triggers the SPR.

Saito et al. (1990), using a new method for investigating the activity of efferent fibers (i.e., microneurography), directly showed that the skin sympathetic nerve activity (SSNA) during a static handgrip exercise was different from the muscle sympathetic nerve activity (MSNA). The authors considered that the central command from the higher centers (i.e., cerebral cortex) increased SSNA. Saito and Mano (1992) also recorded the SSNA and MSNA preceding a handgrip exercise, and showed that HR and SSNA increased before the movement onset when the subject could anticipate the onset of exercise, whereas blood pressure and MSNA did not change. They considered that the excitation of the cerebral cortex by anticipation of exercise makes HR and SSNA increase, and the psychological preparedness to exercise, that is, movement preparation of higher centers, selectively activates or inhibits the sympathetic nerve activities. It is therefore suggested that the sympathetic activity plays an important role in adapting the body to exercise.
APPENDIX B: SOMATOSENSORY N250

The somatosensory N250 is analogous to N2b, which can be measured also with auditory stimulation. The N2b is usually followed by a P3a, and therefore they are often called the N2b-P3a complex. However, when the discrimination between target and nontarget stimuli is performed successfully, the most prominent deflection elicited by deviant/target stimuli is usually P3b. The N200/P300 complex evoked by target tones in oddball paradigms with voluntary responses to the given stimuli has been recorded intracranially from the prefrontal cortex, caudate nucleus, and cingulate gyrus (Kropotov et al., 1995), and also from the anterior (Smith et al., 1990) and posterior cingulate and supramarginal gyri (Halgren et al., 1995). Josiassen et al. (1982) showed somatosensory N230 and P400 deflections evoked by target electric stimuli applied to the index or middle finger. Kujada et al. (1995) recorded auditory N2b-P300 and somatosensory N250-P300 complexes in the selective attention condition where subjects attended to rare auditory and somatosensory deviants and ignored the stimuli of the other modality. Kekoni et al. (1996) showed that the somatosensory N250 was evoked not by deviant stimuli in the ignore condition but by target or deviant stimuli in the attend condition.
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