**Neural mechanisms of attention involved in perception and action:**
**From neuronal activity to network**

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**Abstract** In everyday life, attention is adaptively directed to a stimulus and action in multisensory environments. Recent studies have demonstrated that the functionality of attention and related brain activities are improved by exercise and sports activities. We herein reviewed our previous studies on the neural mechanisms of attention using magnetoencephalography (MEG) and electroencephalography (EEG) (MEEG). MEEG non-invasively records the synchronous activation of neuronal populations from the whole brain of a human as a magnetic field or electric potential with high temporal resolution to the order of milliseconds; and, thus, is a powerful tool for investigating the spatio-temporal dynamics underlying the modulation of real neuronal activities. We presented MEEG data on the neural representations of within-modal, intermodal, cross-modal spatial attention as well as somatic-motor interactions; these were discussed in terms of the effects of attention directed to a stimulus and action on early sensory processing. We also discussed a recent study on attention using a relatively new analysis technique (graph-theoretical or complex network analysis) in human neuroimaging to demonstrate the spatio-temporal dynamics of the functional properties of the human brain network underlying attentional control. These findings support the hypothesis that early sensory processing in modality-specific cortices is regulated, irrespective of the sensory modality, by attentional control signals from the lateral prefrontal cortex, which operates as an important center controlling the flow of information in the human brain.

**Keywords**: attention, magnetoencephalography, electroencephalography, perception, action

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**Introduction**

An important concept in psychology and neuroscience, i.e. attention, has frequently been encountered in sports and exercise sciences, and has historically been examined in psychology and, more recently, in neurophysiology and neuroscience. Previous studies using human electrophysiological approaches, such as electroencephalograms (EEG), reported exercise-induced changes in brain activity that were associated with improved attention-related functions. However, it currently remains unclear exactly what attention is and its underlying mechanisms have not yet been elucidated in detail.

The human brain is bombarded with millions of stimuli from both external and internal sources; therefore, it must decide what information to process. Attention acts as an essential mechanism to select task-relevant information in sensory and motor systems. Attention is also a complicated concept associated with multiple characteristics, including selectivity (selective attention), endogenous, exogenous, top-down, bottom-up, active, passive, processing resource, vigilance, and arousal. A famous functional psychologist, William James (1890), once described “Everyone knows what attention is. 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. Focalization, concentration, of consciousness are of its essence”1). Thus, attention is endogenously and voluntarily directed to various features in both sensory stimuli and actions to select task-relevant information for avoiding an excessive load of information processing when dealing with thousands of sensory and motor signals or, sometimes exogenous and involuntary triggers by dangerous, salient, or informative events. The aspect of quantity is attentional or processing resources allocated to ongoing tasks, the availability of which can be varied by arousal levels. Over the past century, a large number of studies have investigated the mechanisms and functionality of attention in humans. However, Styles (2006) described that despite James’s oft-quoted remark, it would be closer to the truth to say that “Nobody knows what attention is” or at least not all psychologists agree2). Recent advances in neuroimaging techniques, including functional magnetic resonance imaging (fMRI), positron...
emission tomography (PET), magnetoencephalography (MEG), EEG, near-infrared spectroscopy (NIRS), and transcranial magnetic stimulation (TMS), have revealed the neural mechanisms of attention and related cognitive functions. We herein reviewed our previous studies on attention to a stimulus and action using the high-temporal resolution neuroimaging techniques, MEG and EEG, and then discussed how our findings support and evolve previous hypotheses on the neural mechanisms of attention to a stimulus and action.

**Magnetoencephalography (MEG) and electroencephalography (EEG)**

MEG and EEG (MEEG) non-invasively record magnetic and electric neuronal activities in the human brain from an array of extracranial magnetic field detectors or scalp electrodes with high temporal resolution to the order of milliseconds. These techniques have led to a deeper understanding of the modulation of neuronal activity in the time domain, i.e., temporal dynamics. The MEEG signal or waveform is a mixture of waves with different frequencies from near-DC to over 1000Hz. This feature provides another advantage to assessing neuronal activity in the frequency domain in detail. MEEG records real brain activity; it is not an indirect measure of brain activity. This electromagnetic property provides physiologically meaningful temporal resolution, in addition to temporal resolution as measuring devices.

**Cross-modal links in spatial attention**

The neural mechanisms underlying attention have been classically investigated in individual sensory modalities. In the past half century, studies have demonstrated that early sensory responses in audition, vision, and somatosensation are enhanced by attention. Other studies have also suggested various attention-related brain processes such as passive attention, attentive target detection, and the allocation of processing resources. However, we live in a multisensory environment and constantly encounter situations in which attention has to be directed to synchronous and asynchronous sensory inputs from different sensory modalities. Hence, behavioral and neural modulations by attention in multisensory environments need to be examined in order to develop an advanced understanding of functions and mechanisms working in the real world. Recent studies elucidated the neural mechanisms underlying cross-modal links in spatial attention among different sensory modalities. Pioneering work in experimental psychology was conducted by Spence and Driver at the level of behavior. They applied a Posner’s expectancy attention paradigm to examine cross-modal links in spatial attention between vision, audition, and touch. In experimental conditions in which the participant knew the likely target location in space, but not the sensory modality in which the target would appear, the performance of discrimination was better in the likely than in the unlikely target location, and no significant differences were observed between the different sensory modalities. Regarding this phenomenon, fMRI studies identified multimodal areas that were commonly activated regardless of whether attention was directed to vision or audition. Using event-related brain potentials (ERPs), Eimer and colleagues examined the neural correlates of cross-modal links, and revealed the temporal dynamics of cross-modal spatial attention effects. However, temporal resolution is weak in fMRI and PET, while spatial resolution is weak in EEG (ERP).

**MEG studies on cross-modal links in spatial attention**

MEG represents a promising tool for elucidating the spatio-temporal dynamics of neural activities. Therefore, we used MEG to demonstrate the spatio-temporal dynamics of cortical processes underlying a cross-modal link from vision to touch. We employed the so-called selective attention paradigm commonly used in ERP research. A visual or tactile stimulus was presented at the right or left space (or hand) in random order at a random interstimulus interval of 800-1,200 ms (Fig. 1). The visual stimulus (light from a light-emitting diode) was delivered through optical fibers. The tactile stimulus was non-painful electrocutaneous stimulation of the index finger on the right or left hand through ring electrodes attached to the fingers. The stimuli were sometimes presented as a double-pulse stimulus to be detected on the attended side. As a result, there were 8 kinds of stimuli that differed in spatial locations (right and left), sensory modalities (vision and touch), and the number of pulses (single and double). Subjects were asked to discriminate stimuli under four conditions in which the direction of attention varied (left tactile, right/tactile, left/visual, and right/visual attention conditions). For example, they were instructed to focus on the right side and detect the double-pulse visual stimulus by counting the number in the right/visual condition.

The MEG signal was measured with a helmet-shaped 306-channel detector array, which was comprised of 102 identical triple sensor elements. Each sensor element consisted of two orthogonal planar gradiometers and one magnetometer coupled to a multi-SQUID (superconducting quantum interference device), and, thus, provided three independent measurements of the magnetic fields. We analyzed the MEG recorded from 204-channel planar-type gradiometers. Only neural responses to the electrocutaneous single-pulse stimulus (frequently-presented standard stimulus) were analyzed in order to observe a pure selective attention effect that did not include any target-related effect or activity. We computed and measured the magnitudes of the magnetic fields in the sensor space and those of the current dipoles in the source space. We then detected neural responses to somatosensory stimulation
in the primary and secondary somatosensory cortices (SI and SII) and compared them in different attention conditions.

**Within-modal spatial attention effect**

Responses in SII were enhanced in magnitude by spatial attention when touch was task-relevant (Fig. 2), indicating a within-modal spatial attention effect. The within-modal attentional enhancement in SII was consistently observed in past MEG studies, but these studies only dealt with somatosensation and neglected the spatial aspect of attention. Our findings clearly demonstrated that within-modal spatial attention enhanced neural responses at a latency of ~85 ms around human SII without affecting the SI response. The differential sensitivities of SI and SII to attention were also consistent with the above-described MEG and animal studies.

**Cross-modal spatial attention effect from vision to touch**

A similar enhancement in SII responses by spatial attention was noted even when vision was task-relevant (Fig. 2), thereby demonstrating a cross-modal link from vision to touch. The SI response was not significantly modulated by spatial attention. Thus, the cross-modal link in selective spatial attention from vision to touch was associated with somatosensory cortical processing at a latency of ~85 ms in SII, which is primarily a modality-specific cortex. Eimer and colleagues extensively studied cross-modal links in spatial attention using EEG. In their early study, Eimer and Driver used a similar selective attention task to that employed in the present study, and reported that there was no evidence of cross-modal links from vision to touch when touch was completely task-irrelevant (i.e., when vision was completely task-relevant), while cross-modal links were detected when vision was of primary and touch was of secondary relevance to the task. They considered these findings to be consistent with a behavioral study by Spence et al. The behavioral study of visual-tactile cross-modal links by Spence et al. revealed more rapid and accurate responses to both vibrotactile and visual target stimuli when the target modality was not cued, but the likely target side was cued prior to the target stimulus, than when the unlikely target side was cued or a neutral cue was presented. In their later studies using a cueing task that was different from the earlier one, Eimer et al. reported the existence of cross-modal links from vision to touch. We here found a new cross-modal spatial attention effect using MEG even when touch was completely task-irrelevant in a selective attention task, similar to the early study by Eimer and Driver. In addition, the cross-modal spatial attention effect was observed at an earlier latency than that reported in EEG studies using a cueing task. This may have been due to the advantages of MEG. Thus, we demonstrated a neural representation of a cross-modal link in spatial attention from vision to touch.

**Cross-modal spatial attention effect from touch to vision**

We subsequently examined the oppositely-oriented effect of spatial attention, i.e., a cross-modal link in spatial attention from touch to vision. We analyzed visual evoked magnetic fields (VEFs) in the same experiment. This analysis was conducted in both the sensor space and source space. We performed a minimum norm estima-
tion, a common method used to estimate distributed current sources in the brain, in order to examine attentional modulation in the whole brain. We demonstrated within-modal, intermodal, and cross-modal spatial attention effects on a visually evoked response (VER) at the occipito-temporal areas, and the cross-modal attention effect was localized at the temporo-parietal junction (TPJ) (Fig. 3). Other attention effects were localized in more distributed occipito-temporal regions and even in lateral frontal areas (inferior and middle frontal gyri). Thus, we found bidirectional links in spatial attention between vision and touch.

Hubs for attentional control

We demonstrated the bi-directional, cross-modal attentional modulation of stimulus processing as indexed by attentional increases in neuronal responses to stimuli from different sensory modalities. This finding implied that there may be a center sending top-down attentional signals to control stimulus processing in sensory-specific and multisensory cortices. Although the prefrontal and posterior parietal cortices have been suggested as classical candidates, this has been based on studies on patients with lesions in these areas and activation studies in normal subjects, which are not a demonstration of centers of the ‘network’, but that of functional localization. Recent interregional connectivity studies reported that the prefrontal and some higher-order areas may send top-down attentional signals to low-level cortical hierarchies, but these studies also did not examine network properties in terms of network science. What and where is the center of the human brain network controlling spatial attention? When and how does it act? In order to address these questions, we employed a sophisticated analysis technique, a graph-theoretical analysis (complex network analysis)\(^{41}\), to the MEG dataset recorded during the performance of a cue-target multisensory attention task in which subjects attended to auditory and tactile target stimuli on the left or right side as informed by a visual cue stimulus\(^{42}\). We analyzed the MEG signal in the cue-target interval, which was defined as the period of attentional control. The anal-

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Fig. 2  Attentional modulation of tactile-evoked responses. The left panel indicates analysis of the response to left hand stimulus (LHS), and the right panel to right hand stimulus (RHS). (A) The across-subject mean location of ECDs superimposed on a three-dimensional MRI scan in one subject. (B) Location of ECDs superimposed on a two-dimensional MRI scan. ECDs were estimated to be located in the posterior bank of the central sulcus, corresponding to SI, and bilaterally in the upper bank of the sylvian fissure in the left and right hemispheres, corresponding to the bilateral SII. (C) The time course of the ECD moment in the SI and SII, as indicated by multidipole analysis (grand-averaged waveform across subjects). ECD: equivalent current dipole, MRI: magnetic resonance imaging, A: Anterior, P: Posterior, L: Left, R: Right, Ro: Rostral, Ca: Caudal, SIIR (SIIL): Secondary somatosensory cortex in the right (left) hemisphere, SIIc (SIIi): Secondary somatosensory cortex in the hemisphere contralateral (ipsilateral) to the stimulus side, GOF: goodness-of-fit value.
ysis used here provided various network properties, and, thus, the application of this to the MEG dataset enabled us to examine the spatio-temporal dynamics of functional network properties in the human brain. The findings obtained revealed global hubs in the prefrontal and sensorimotor cortices and decreased functional segregation during attentional control (Fig. 4), indicating that prefrontal and sensorimotor cortices acted as an important center for the control of information flow during attentional control. We also showed a change in the distribution of beta desynchronization by spatial attention, which is another sign of attentional control.

**Modality-dependent and independent mechanisms of spatial attention**

Three hypothetical systems for the organization of endogenous spatial attention are possible for modality dependency. Separate modality-specific systems may operate independently of their respective representations of the visual and tactile (and auditory) spaces. A single supramodal attentional system that allocates attention to locations in space regardless of the modality of the target being attended may modulate perception and neural activity as a function of location across sensory modalities. A separable modality-specific attentional system exists, but with links such that visual spatial attention is more likely to result in tactile attention to the corresponding location in the tactile space, and vice versa. Since we found cross-modal attentional modulations, the separate modality-specific system is not suitable for the organization of spatial attention. In addition, we identified a difference in cross-modal attentional modulation between tactile-evoked and visual-evoked responses, with vision-to-touch spatial attention effects being greater than touch-to-vision effects. This finding is consistent with a separable-but-linked system. Other researchers also provided evidence to support this system from different perspectives such as behaviors, ERP, and TMS. Moreover, our MEG study using time-frequency analysis and graph-theoretical analysis showed that beta oscillations and network properties may be associated with attentional control, thereby supporting a modality-independent attention system. A previous study also reported that some ERP components were associated with attentional control. Consequently, we proposed a hybrid system consisting of a separable-but-linked system for the attentional modulation of stimulus processing and a modality-independent system for attentional control.

**Attention to action**

Our voluntary action inevitably involves attention directed to the action itself or to the body parts involved in the action. Accordingly, directing attention to the action may also modulate sensory processing at the early stages in SI and SII, as well as attention to stimulus, as discussed in previous sections. The direction of attention to an action is assumed to work during the execution, preparation, or imaging of the movement of a specific limb. A large body of evidence has confirmed the modulation of somatosensory cortical activity under these conditions. Electric or magnetic responses to somatosensory stimuli were previously shown to be modulated by repetitive movements of the finger involved in the stimulated body parts. This response reduction started before the
onset of movements or during the preparation of movements\textsuperscript{49-55}. This response reduction also exhibited selectivity, i.e., the response was selectively reduced when the stimulated body parts were moved or prepared for movement. This somatic-motor selectivity is consistent with the general properties of attentional selectivity in the sensory domain. Therefore, we hypothesized that attention to an action has comparable effects on neuronal responses in the modality-specific cortex as attention to a stimulus, similar to SII.

**MEG study on attention to an action**

We employed a choice reaction paradigm with warning and imperative signals to examine the effects of attention directed to an action on somatosensory cortical responses\textsuperscript{56}. A visual warning signal was followed after 2 s by a somatosensory imperative signal. The interval between successive warning signals varied randomly between 4 and 6 s. The visual warning signal was either of upward, right-pointed, and left-pointed arrows, which were presented in a random order and at an equal probability on a screen in front of the subjects at a distance of 2 m through a digital light processing projector. The electrical stimulation was delivered to the right median nerve at the wrist to trigger a voluntary movement and evoke a magnetic response. The warning signal informed subjects of the action to be prepared for and actually executed. Subjects were instructed to prepare to extend the second digit of the right hand without any muscle contraction when the warning signal was a right-pointed arrow, and to extend the digit as fast as possible when the imperative somatosensory signal was presented (right-hand reaction trial). If the warning signal was a left-pointed arrow, they first prepared and then extended the second digit of the left hand on presentation of the imperative signal (left-hand reaction trial). An upward arrow instructed subjects to execute no action in that trial (control trial). When no somatosensory signal was presented (catch trial), the subjects refrained from extending the digit even when the preceding warning arrow pointed in one direction. The procedure and methodology of MEG measurement was the same as that in the above-described study on cross-modal links.

**Efferent modulation of SI and SII responses**

The short-latency SI response that peaked 35 ms after the somatosensory signal was reduced when the signal triggered a voluntary movement (Fig. 5). This reduction was caused by a centrifugal mechanism in which a motor-related efferent signal suppressed a neural response through a similar mechanism to cortico-cortical inhibition because the finger extensor muscle was voluntarily activated after the response. In the forewarned reaction time task, a contingent negative variation (CNV) was generated between warning and imperative signals, which reflected anticipation and movement preparation\textsuperscript{57}. This preparatory neuronal activity was observed in the premotor area (PMA), supplementary motor area (SMA), primary motor area (MI), and prefrontal area (PFA). The interconnections between these areas and the SI are well known. Therefore, we speculated that preparatory neuronal activities in these areas for an upcoming somatosensory signal inhibited the short-latency neuronal response in the SI via cortico-cortical connections. Using a similar experimental paradigm, our previous EEG studies found that the electrical neuronal responses, N30-P30, were reduced without alterations in subcortical and primary cortical responses\textsuperscript{49,52,53}, which is consistent with this study showing the absence of changes in N20m. Therefore, our studies indicated that human early cortical processing of a task-relevant somatosensory signal was regulated at the SI by a centrifugal mechanism caused by neuronal activities before that signal.

Bilateral SII responses in the sylvian fissure were increased 80 and 95 ms after the somatosensory signal when the signal triggered a voluntary movement (Fig. 5). The centrifugal mechanism may have contributed to these increased responses as well as decreased responses in the SI. Furthermore, the enhancement observed in the SII was marked when the somatosensory signal triggered movement of the hand ipsilateral to the stimulation. No significant modulation of the SII response was detected when movement was executed with the hand contralateral to the stimulation. Under this reaction condition, attention had to be directed to both hands for stimulus detection and voluntary movement. Therefore, the direction of attention to the stimulation itself may not have been the main factor causing the enhanced response in the present experimental paradigm. One functional explanation for enhanced responses in the SII is top-down signal amplification in the SII to extract task-relevant somatosensory signals from the body parts involved in the action. Our previous EEG studies also assumed that the enhanced response observed at approximately 80-100 ms was associated with this signal amplification, and may be referred to as the effect of directing attention to the body parts involved in an action\textsuperscript{49,52,53}. Regarding the somatosensory cortical hierarchy, the SII forms a ventral stream\textsuperscript{58}, which projects to the PM\textsuperscript{59,60} and PFC\textsuperscript{61}, and may be associated with the fine discrimination and identification of somatosensory inputs\textsuperscript{62}. The idea of signal amplification in the SII appears to be consistent with this notion.

**Summary**

The findings of our MEEG studies revealed how attention to a stimulus and action modulated the synchronous activation of neuronal populations in the SI and SII in the early stages of cortical processing. Regarding attention to a stimulus, our studies demonstrated the neural
representations of within-modal, intermodal, and cross-modal spatial attention effects in vision and touch. One of the centers sending top-down attentional control signals to stimulus processing in the modality-specific cortices is the lateral prefrontal cortex, as revealed by complex network analysis. Attention to an action also induced an enhanced response in the SII to a task-relevant somatosensory signal. The pattern of these response modulations is consistent with a cortical attentional regulation mechanism in which attention to a stimulus and action controls neural responsiveness in modality-specific cortices in the early stages to a task-relevant sensory input. We proposed a hybrid system consisting of a separable-but-linked system for the attentional modulation of stimulus processing and a modality-independent system for attentional control, with the latter regulating the former.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this article.

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