Perceiving the passage of time is an essential ability for humans and animals. Here we used magnetoencephalography and investigated how our internal clock system in the brain converts sensory experiences into their time representations. We focused on neural activities in the high-level visual areas of human subjects when they saw visual patterns and estimated the duration of their presentation. The activities in the visual areas could give us neural indices about when subjects perceived the appearance and disappearance of visual patterns, thus enabling us to measure the stimulus duration “in the brain.” Comparing these neural indices of time with subjective durations of stimuli measured psychophysically, we showed that, under some circumstances, these 2 durations can be dissociated in the opposite directions: although the neural index signals a “longer” interval of a stimulus over another one, it is perceived as “shorter” in subjective time scale. Instead, we found that these subjective intervals are closely linked to the strength, not timings, of neural activity evoked by visual patterns. Our results indicate that “nontemporal information” of perceptual neural activity, such as the strength (not latency) of neural responses, can influence the shaping of time representations in our brain.

Keywords: human, magnetoencephalography, neural adaptation, temporal processing, ventral pathway, visual

Introduction

Sensations of time play a crucial role in many aspects of our daily lives (Gibbon and others 1997; Matell and Meck 2004; Nobre and O’Reilly 2004). A number of behaviors such as performing complex movements, listening to music, and speaking a language are all built on a precise motor and perceptual time processing in the millisecond-to-second range (Harrington and Haaland 1999; Macar and others 2002; Lewis and Miall 2003b; Ivory and Spencer 2004; Mauk and Buonomano 2004). In spite of the obvious importance of representation of time, previous psychophysical and neurobiological studies have shown that our sensation of the time interval to a perceptual event (e.g., illumination of a photo diode or presentation of a tone) can be significantly modulated by various factors other than the physical duration of that event: attention (Macar and others 1994; Brown 1997), modality (Wearden and others 1998), disease (Malapani and others 1998), or drugs (Meck 1996; Rammayer 1999), etc. For example, when human subjects were asked to estimate the duration of diode illumination and do a nontemporal task (e.g., detection of an increment in light intensity) simultaneously (dual-task paradigm), they judged the duration of illumination to be shorter than that under the single-task condition (duration task only) (Casini and Macar 1997; Coull and others 2004). This result can be interpreted as an effect of attention divided from the temporal task to the nontemporal task, which interrupts the ticking of the “internal clock” (Treisman 1963) in the brain. As the adage “time flies when you’re having fun,” these studies indicate that our system for temporal processing is not always an exact one that faithfully mirrors the actual timing of the beginning and end of an event, although the precise neural mechanisms behind the construction of subjective time representations remain unknown.

In the present study, we used magnetoencephalography (MEG) and focused on the temporal information of a visual stimulus represented in high-level visual regions of the human brain. Previous studies have reported that MEG detects the electromagnetic responses of the visual areas induced by the onset and offset of visual stimulus (onset and offset responses), which have been thought to reflect the perceptual timing of the beginning and end of the stimulus. In the framework of the pacemaker-accumulator model (a representative theory of the internal clock system in the brain), these onset and offset timings in the brain play an important role in shaping the temporal representation of that stimulus because several studies have assumed a “switch” (or “gate”) component between the pacemaker and accumulator in this model (Gibbon and Church 1984). This switch allows neural pulses from the pacemaker to flow into the accumulator when the brain perceives the onset of the stimulus that should be timed and cuts the pacemaker-accumulator connection when the stimulus ceases (and the total amount of pulses accumulated at the end of the interval determines our subjective duration). Indeed, a previous study has reported that the opening and closing latency of this switch differ between visual and auditory modalities, which produces the high accuracy (low variability) of time estimation in auditory over visual domains in the human subjects (Wearden and others 1998). These studies suggest that the hypothesized switch of the internal clock receives the temporal information from sensory areas of each modality, and thus the interval between the onset and offset responses in the sensory areas is predicted to be closely related to the period during which the neural pulses are accumulated for the calculation of subjective time representations. Is there any correspondence between actual onset-offset interval in visual activity and our subjective duration of the presented stimulus? If not, what aspects of visual activity were used by the internal clock system to make temporal representations? Our results would provide insight into how the clock in the brain converts sensory information into the time representations of perceptual events.

Another characteristic of the present study is that we observed neural activities in the higher visual regions rather than the lower visual cortex. This is related to our aim in this study of investigating the brain mechanisms that construct “subjective” time representations. As described above, 1 major
factor affecting the subjective time interval of a given stimulus is “attention.” Previous neurophysiological and neuroimaging studies have shown that the effect of attention on neural activity (such as attentional enhancement or attentional suppression) is stronger in higher sensory areas rather than lower regions (Cook and Maunsell 2002; Saenz and others 2002). These previous findings lead us to predict that the subjective (not physical) duration of a visual stimulus would be more closely associated with the neural activity in higher rather than lower visual areas. Thus, as an initial step to investigate the relationship between sensory activities and subjective time representations, we focused on the higher areas in the human brain and studied the changes in neural dynamics of these regions when the subjective time percept of a physically identical stimulus was manipulated.

Materials and Methods

Subjects
The present study consisted of 2 (behavioral and MEG) sessions. Fifteen and thirteen healthy volunteers were used in the behavioral and MEG experiments, respectively (11 of them participated in both). All subjects had normal or corrected-to-normal visual acuity. Informed consent was received from each subject after the nature of the study had been explained. Approval for these experiments was obtained from the ethics committee of the National Institute for Physiological Sciences, Okazaki, Japan.

Stimuli and Task
In both behavioral and MEG sessions, subjects viewed 2 visual stimuli sequentially presented in the central visual field: standard (1st stimulus) and test (2nd stimulus). Each stimulus was either “<” or “>” (size: 3.4 × 3.8 degree, Fig. 1A), and there were 2 types of trials according to the combination of the 1st and 2nd stimuli. In 1 half of the trials, the same stimulus was repeatedly presented as standard and test (e.g., “<” → “<”, SAME trials). The 2 stimuli were different in the other half (e.g., “<” → “>”, DIFF trials). For both standard and test stimuli, the number of presentations of each stimulus (“<” or “>”) was counterbalanced between SAME and DIFF trials. The duration of the standard stimulus was either 600 or 800 ms in the behavioral session, whereas it was fixed at 600 ms in the MEG session. As the duration of the test stimulus, we selected several time intervals in and around the standard duration (500–700 ms for the 600-ms standard and 700–900 ms for the 800-ms standard). The temporal delay between standard offset and target onset was variable from 450 to 650 ms. Subjects were asked to compare the duration of the test stimulus with that of the standard stimulus, neglecting the stimulus shape (left- or right-faced) or the shape congruency between standard and test. They pressed 1 button when the test duration was shorter than the standard duration and another button when it was longer. In both behavioral and MEG sessions, a single experimental run comprised 72 trials and was repeated 6 times in 1 experiment. In the behavioral session, the duration of the standard stimulus was 600 ms in 1 half of the trials and 800 ms in the other half, whereas all trials during the MEG experiment had a 600-ms standard. For each standard duration, there were 8 (4 test durations × SAME or DIFF) or 6 (3 test durations × SAME or DIFF) types of trials in behavioral and MEG sessions, respectively (Fig. 1D), and all these trials were randomly intermingled in each experimental run. Subjects were naive about the experimental design and thus unaware that the standard and test durations were physically the same in some trials of the MEG session. Due to a technical problem, the behavioral data for one of the 13 subjects could not be recorded in the MEG session.

Stimulus Presentation Methods in the MEG Session
Whereas the behavioral patterns in the behavioral session (“<” or “>”) were composed of white pixels against a black background on a computer screen, these patterns were presented through our random dot blinking (RDB) technique (Okusa and others 1998; Noguchi and others 2004) in the MEG session, in order to isolate the neural activity in occipitotemporal higher visual regions related to shape perception or object recognition (Grill-Spector and others 1999; Kourtzi and Kanwisher 2001). With this method, visual patterns such as “<” and “>” were presented at the center of a black-and-white random dot field (60 × 60 dots, 6 × 6 degrees). Although all dots in the field flickered continuously in the resting period, a subset of dots making up the visual pattern became static during the pattern presentation period, whereas the other dots (outside the visual pattern) remained dynamic. This static-dynamic contrast enabled observers to perceive the shape of the visual pattern. Because the ratio of white and black pixels was fixed (white:black = 1:3) throughout both periods, the mean luminance of the field was always the same. One advantage of this technique is that those RDB visual patterns can induce the neural activity of higher visual areas in the ventral pathway without evoking significant responses in the V1 area, the region especially sensitive to luminance change of the stimuli. Our previous study has shown that this stimulation paradigm effectively inhibits the neural responses from V1 and allows us to focus on higher visual activities related to shape recognition (Okusa and others 1998). Indeed, it was reported that RDB visual patterns induced 1 simple neuromagnetic response at a peak latency of ~300 ms, the signal source of which is estimated to lie in the occipitotemporal area around the fusiform gyrus. Other details on the RDB method were described elsewhere (Noguchi and Kakigi 2005).

MEG Recordings and Data Analyses
Visual-evoked fields (VEFs) in response to standard and test stimuli were recorded with a helmet-shaped 306-channel MEG system (Vectorview, Elekta Neuromag, Helsinki, Finland), which comprised 102 identical triple sensor elements. Each sensor element consisted of 2 orthogonal planar gradiometers and 1 magnetometer coupled to a multi-superconducting quantum interference device and thus provided 3 independent measurements of the magnetic fields. In the present study, we used MEG signals recorded from 204-channel planar-type gradiometers. The signals from these sensors are strongest when the sensors are located just above local cerebral sources (Nishitani and Hari 2002). To prevent neuromagnetic artifacts induced by eye blinking, a brief interval (2 or 5 s) was interposed every 4 trials, and subjects were asked to blink their eyes within that period. Eye position was also monitored using an infrared eye tracker (Iscan Pupil/Corneal Reflection Tracking System, Cambridge, MA, Fig. 1C). The MEG signals were recorded with 0.1–200 Hz band-pass filters and digitized at 600 Hz.

For data analyses, we conducted the selective averaging of visual neuromagnetic responses in 6 conditions (3 test durations × SAME or DIFF). The data from “72 trials at maximum were averaged in each condition of each subject. In all conditions, the VEFs for standard and test stimuli were calculated separately, time locked to the onset of each stimulus. The averaging epoch ranged from 100 ms before to 1050 ms after the onset with the prestimulus period (initial 100 ms), used as a baseline. Epochs in which signal variation was larger than 3000 fT/cm were excluded from the averaging.

To detect the occipitotemporal signals related to the recognition of visual patterns (the 300-ms component reported previously), we took the sensor of interest (SOI) approach described in previous MEG studies (Liu and others 2002; Noguchi and others 2004). First, apart from the standard and test VEFs in the 6 conditions described above, we averaged MEG responses to the standard stimulus in all trials (n = 432 at maximum) for each subject (grand-standard VEF, Fig. 2A). On this waveform of high signal-to-noise ratio, we selected the SOIs in the present study from 204 planar channels according to the following criteria: 1) the peak deflection lies 200–400 ms after the stimulus onset and 2) a significant deflection (>2 standard deviation of the fluctuation level in the baseline period of each channel) continues for at least 100 ms centering on the peak latency. These criteria were based on our previous results reporting the fusiform activation at a latency of ~300 ms (Okusa and others 1998). An average of 182 SOIs were selected for each subject (Fig. 2B). Using this SOI information, we then averaged standard/test VEFs (that were initially calculated for each of the 6 conditions) across all SOIs, producing an across-SOI VEF for each condition of each subject. Because there were 2 types of SOIs showing positive and negative deflections, VEFs on negative SOIs were flipped before across-SOI
averaging to match the polarities of all SOIs (Liu and others 2002). On these across-SOI VEFs, we searched for onset and offset peak responses of these waveforms, the neural signals encoding the stimulus appearance and disappearance, respectively. Onset peak was defined as the largest deflection within the time period of 200–500 ms after the onset of standard or target stimuli, whereas offset peak was sought in the time window of 700–1050 ms after the stimulus onset.

The SOI analysis described above has several advantages covering the weakness of a conventional dipole modeling analysis. First, in the dipole analysis, clear neuromagnetic responses above a certain number of MEG channels (usually, more than 20) are necessary to estimate a reliable dipole source. Consequently, a small number of channels is omitted from the dipole analysis, even when these channels have clear neuromagnetic responses that should be evaluated. Second, the data in a dipole analysis are somewhat dependent on the selection of MEG channels used for dipole estimation. A small change in the selection of channels occasionally produces a dipole waveform slightly different from the original. The SOI approach used in the present study is free from these problems because 1) there is no lower limit of channel numbers and 2) the selection of the subset of channels is based on fixed criteria. However, the spatial location of the signal source is not made clear using only the SOI analysis.

To resolve this issue, we also conducted single equivalent current dipole (ECD) estimations on the grand-standard VEFs of each subject.

**Figure 1.** Scheme and results of the duration discrimination task. (A) A sequence of 1 trial in the SAME and DIFF conditions. Initially, a fixation point appeared for 500 ms in the central visual field of subjects. Two visual stimuli (\(<\) or \(>\)) were then sequentially presented with a 450- to 650-ms delay between the offset of the 1st stimulus (standard) and onset of the 2nd stimulus (test). (B) Results of the duration discrimination task in behavioral (left) and MEG (right) sessions. The probability that subjects responded long (% long) was plotted for each test duration (mean ± standard error across subjects). Note that the % long was generally lower in SAME trials (broken lines) than DIFF trials (solid lines). *P < 0.05, **P < 0.01, ***P < 0.001, paired t-test. (C) Eye position monitored by a near-infrared tracker during the MEG session. The vertical (left) and horizontal (right) changes of averaged eye position in response to the 600-ms test stimulus are shown (broken: SAME, solid: DIFF). Zero on the abscissa represents the onset of the test stimulus. Because there were 2 types of trials in the DIFF condition (\(<\) \(\rightarrow\) \(\rightarrow\) and \(\rightarrow\) \(\rightarrow\) \(\rightarrow\)) that might produce a visual saccade with opposing directions, we averaged the absolute values of eye position signals to avoid the cancellation of the signals between these 2 trials. Almost identical results were obtained when we used nonabsolute values of position signals.
We adopted a spherical head model based on individual magnetic resonance images (Hamalainen and others 1993). The locations of ECDs best explaining the distribution of the magnetic fields over at least 20 channels around the signal maxima were estimated using the least square method. We accepted only dipoles that account for at least 80% of the field variance at the peak (Nishitani and Hari 2002).

Analyses on BuildUp Activity in MidFrontal Region

Based on previous studies reporting the "temporal accumulator" waveforms in the supplementary motor area (SMA) that represent subjective durations of presented stimuli (Macar and others 1999; Pfeuty and others 2003), we analyzed in Figure 6 the slow buildup neural activity over the frontocentral region. The MEG data in 24 planar sensors (shown in Fig. 2A) were averaged together, and the mean signal amplitude 450-550 ms after the stimulus onset was compared between SAME and DIFF. The results in offset response latency (Fig. 4C) suggest that neuromagnetic signals in this period include no offset responses. To precisely evaluate the amplitude of buildup waveforms, baseline correction was applied to the data 350-450 ms after the stimulus onset.

Results

Behavioral Results

The results of the duration discrimination task (probability that subjects answered long, % long) are shown in Figure 1B. As expected, the percentage of "long" responses was elevated along

(Fig. 3A). We adopted a spherical head model based on individual magnetic resonance images (Hamalainen and others 1993). The locations of ECDs best explaining the distribution of the magnetic fields over at least 20 channels around the signal maxima were estimated using the least square method. We accepted only dipoles that account for at least 80% of the field variance at the peak (Nishitani and Hari 2002).
with the increase in test duration. A notable thing was that "% long" was generally lower in the SAME condition than in the DIFF condition, although this difference became less distinct when the test duration was too far from the standard duration (e.g., at 500 and 700 ms in the 600-ms standard condition). In the behavioral session (left panel of Fig. 1B), a 2-way analysis of variance (ANOVA) of test duration × stimulus congruency (SAME or DIFF) indicated a highly significant main effect of congruency for both the 600- and 800-ms standards (600-ms standard: \( F = 9.62, P < 0.005 \); 800-ms standard: \( F = 31.14, P < 0.001 \)). A difference between SAME and DIFF was also observed during MEG measurements (right panel of Fig. 1B, \( F = 16.02, P < 0.001 \), main effect of congruency). These results indicate that test stimuli were perceived as shorter in the SAME trials than in the DIFF trials, particularly when the subjects’ judgments became ambiguous due to the duration adjacency between test and standard. One should note that this effect cannot be explained by the "chronostasis" reported in previous studies (Yarrow and others 2001). Chronostasis refers to the lengthening of the subjective duration of the visual stimulus after a saccadic eye movement and is commonly experienced as the "stopped clock" illusion in daily lives (i.e., when we make a saccade to a silently ticking clock, the second hand is perceived to take longer than usual to move its next position). Whereas previous studies have shown that the chronostasis is induced by the visual saccade (but not a shift of spatial attention) to the target stimulus (Yarrow and others 2001, 2004), no difference of eye position in response to the test stimuli was observed between SAME and DIFF in the present study (Fig. 1C), indicating that the judgment bias observed in the present study should not be attributed to chronostasis.

### Visual Neural Activity during the Duration Discrimination Task

We recorded by MEG the neural activity of visual regions when this time illusion occurred. As shown in Figure 2A, the standard and test visual patterns induced clear deflections of the neuro-magnetic waveform mainly in posterior lateral regions of both hemispheres, the latency of which was typically ~300 ms (Fig. 2B). Single ECD analysis indicated that the signal sources of these deflections were located in the bilateral occipitotemporal regions in the visual ventral pathway (Fig. 3A), the areas of the brain related to shape perception or object recognition of visual stimuli (Grill-Spector and others 1999; Kourtzi and Kanwisher 2001). If the shortening of the subjective duration of the test stimulus in SAME is produced by the shape consistency of the 2 visual stimuli, it is predicted that the stimulus congruency induces some form of neural change in these areas, which affects the temporal representation of the test. We evaluated these high-level visual activities in each subject by calculating an absolute-mean waveform across sensors where the 300-ms component was evident (across-SOI VEFs). As in the grand-averaged (\( N = 13 \)) results in Figure 3B, those waveforms simultaneously showed 2 types of neural responses to the visual stimuli: onset and offset responses. The onset responses were observed in approximately 300 ms and were not sensitive to the stimulus duration, indicating that these responses serve as a neural "trigger" signal representing the stimulus onset itself. On the other hand, the offset responses were generally smaller than the onset responses, and their latencies showed a gradual increase along with the stimulus duration, encoding the off timing of visual stimuli. The temporal intervals of these 2 responses would play an important role in determining subjective durations of visual patterns.

We investigated these responses in the higher visual areas when the stimulus repetition changed the subjective duration of the test stimuli. Figure 4A presents the neural time series of 1 representative subject (upper panels) and grand average of 13 subjects (lower panels) for standard (left side) and 600-ms test (right side) stimuli. Although neural responses to standard were almost identical between SAME (blue lines) and DIFF (red lines) trials, the onset response to test stimuli reached a maximum significantly earlier in SAME than in DIFF trials, indicating that the test stimuli began to be processed in the brain more rapidly in SAME trials than in DIFF trials. Also, there was an attenuation of the vertical deflection of neural activity in SAME relative to DIFF. This acceleration and attenuation of higher visual responses is called "neural adaptation" (Henson 2003; Noguchi and others 2004), a well-known mechanism that facilitates the neural processing of repeatedly presented stimuli relative to unRepeated ones (i.e., the visual stimuli presented more than once are detected faster and processed more effectively than those in the 1st presentation, for review, see Henson 2003).
Figure 4. Visual neuromagnetic waveforms during the duration discrimination task. (A) Across-SOI VEFs for standard (left) and test (right) stimuli in a representative subject (upper panels) and the grand average of 13 subjects (lower panels). Blue and red lines represent the neural time series in SAME and DIFF trials, respectively. (B) Mean (±standard error [SE] across 13 subjects) peak amplitudes and latencies in standard (left) and test (right) responses. In the test response, SAME trials (blue) showed a significantly smaller peak amplitude and latency than DIFF (red). (C) Offset latencies (mean ± SE) in test responses. (D) Onset–offset latency differences (neural intervals, solid lines) in test responses and the results in % long (broken lines, identical data to Fig. 1B). In the right panel, the mean (±SE) values of SAME minus DIFF in the 3 test durations were plotted for both neural interval and % long. *P < 0.05, **P < 0.01, 1-group t-test. Note that SAME (blue) trials induced a longer neural interval in the brain compared with DIFF (red) trials, whereas % long was significantly smaller in SAME than in DIFF.
the test response, 2-way ANOVAs (Fig. 4B, right) indicated a highly significant main effect of congruency (SAME < DIFF) both in the peak latency and in the amplitude of the onset response (peak latency: $F = 15.19$, $P < 0.001$; peak amplitude: $F = 17.64$, $P < 0.001$), whereas no significant effect was observed in the standard response (peak latency: $F = 0.21$, $P = 0.65$; peak amplitude: $F = 0.54$, $P = 0.47$) (Fig. 4B, left).

We then investigated neural characteristics of the offset responses. In contrast to the onset response modulated by the stimulus congruency, the latency and amplitude of the offset responses to the test stimuli did not differ between SAME and DIFF (main effect of congruency, peak latency: $F = 0.24$, $P = 0.63$; peak amplitude: $F = 0.17$, $P = 0.68$), although the peak latency was significantly affected by the duration of test stimuli (Fig. 4C, $F = 4.55$, $P < 0.05$ for main effect of test duration). As a result, the time interval between onset and offset peak latencies (called the “neural interval” hereafter) for the test stimuli became significantly longer in SAME than DIFF trials (solid lines in the left panel of Fig. 4D) because the onset signals reached visual areas earlier in SAME than DIFF (Fig. 4B, right), whereas neural responses to stimulus offset did not differ between SAME and DIFF (Fig. 4C). A 2-way ANOVA (congruency × test duration) on neural intervals revealed a significant main effect of congruency (SAME > DIFF, $F = 5.69$, $P < 0.05$). Together with the subjects’ performance of the duration discrimination task, these data indicated a counter-intuitive result regarding the time-processing mechanisms of humans: the SAME stimulus, which has a longer onset-offset interval in the brain, was perceived as shorter behaviorally (Fig. 4D). This finding challenges the ordinary concept of time perception that we estimate the temporal length of an event by measuring the delay between the beginning and end of it.

**Neural Correlates of Subjective Time Interval**

Then, what aspects of neural activity determine our sensation of time? To address this issue, we performed another type of selective averaging of MEG data, comparing the trials in which the subject answered “short” with those in which they answered “long.” Figure 5 shows neural responses in these short and long trials of 600-ms test stimuli (in this analysis, we used the data in the 600-ms condition only because the results in Fig. 1B indicate that the perceptual shift became less distinct when the test duration was too different from the standard duration). A marked difference between these 2 types of trials was observed in the peak amplitudes of onset responses, rather than peak latencies (Fig. 5B). We also calculated the onset–offset interval of short and long trials. The results are shown in the right panel of Figure 5B. Although these intervals became longer in SAME than DIFF ($t = 2.16$, $P < 0.05$) because the onset latency of the SAME trials was selectively shortened by the neural adaptation,
the difference between short and long trials was not significant ($t = 0.08, P > 0.9$). These results suggest that a parameter of neural activity linking to subjective duration is the amplitude of VEFs and that the visual stimulus evoking the smaller response in higher visual regions tends to be perceived as shorter. This view provides 1 possible explanation for the paradoxical results in Figure 4D (remember that the test in SAME trials, which was judged shorter behaviorally, induced neural activities with smaller peak amplitudes than DIFF). And if this is true, a prediction derived is that the individuals who showed larger amplitude reductions in higher visual responses by the neural adaptation (Fig. 4B, lower panels) should be more subject to time illusion, that is, more likely to judge the SAME stimulus as shorter compared with DIFF. We therefore calculated an interindividual correlation between reductions in peak amplitude and % long (Fig. 5C). A significant correlation was observed between peak amplitude and % long ($r = 0.60, P < 0.05$), but not between peak latency and % long ($r = -0.03, P > 0.9$) or between neural interval and % long ($r = 0.28, P > 0.3$), demonstrating a close relationship between the strength of neural activity and subjective time intervals.

**Buildup Activity in Frontocentral Regions**

The data above indicated that the differences in intensity of the visual response do modulate the subjective duration of the visual stimuli. The present results are, however, somewhat inconsistent with previous studies, many of which have shown that the temporal representations of humans are created in the neural network over an extensive area that includes the basal ganglia, SMA, and thalamus (Gibbon and others 1997; Coull and others 2004; Matell and Meck 2004), not in the sensory areas themselves. Specifically, the SMA region has emerged as one of the strongest candidates for a “pulse accumulator” in the temporal processing system (Macar and others 1999; Pfeuty and others 2003; Coull and others 2004), which stores the internal neural pulses while we measure the duration of a certain sensory event. The total number of pulses accumulated at the end of the event is thought to determine our subjective duration of that event. Indeed, an electroencephalography (EEG) study by Macar and others (1999) showed that the amplitude of slow buildup activity recorded from frontocentral regions is positively correlated with subjective (not physical) interval defined by auditory stimuli, suggesting that the neural amplitudes in these regions reflect an output of the temporal accumulator system. Therefore, 1 possible explanation for the difference between present and previous results is that the weaker response in visual areas also induces smaller activation in the accumulator system including the SMA, leading to the perception of a shorter duration.

To examine this possibility, we investigated the buildup activity in the present study by averaging the MEG waveforms in 24 sensors over the frontocentral region (see, Fig. 2A). Consistent with previous studies (Macar and others 1999; Pfeuty and others 2003), slow-increasing neural waveforms were observed after the onset responses to the test stimuli (shaded area in Fig. 6A, the signal source of these waveforms was shown in Fig. 6D). As expected, the test stimulus in SAME induced neural activity of smaller amplitude than that in DIFF also in this region. A 2-way ANOVA (congruency × test duration) on mean signal amplitude during 450–550 ms after the onset indicated a significant main effect of congruency (Fig. 6C, $F = 14.14, P < 0.001$) (We selected this time interval to avoid the possible effects of offset responses in this region. We confirmed that the results were unchanged when we used different intervals for analysis). Furthermore, a significant correlation ($r = 0.60, P < 0.05$) was found between the changes in intensity (DIFF–SAME) of VEF from higher visual areas and those of the buildup waveforms in the SMA (Fig. 6D). These results support the hypothesis that neural activities in higher visual areas and SMA regions are closely linked, and the weaker activity in higher visual areas thus leads to less output in the temporal accumulator in the SMA, resulting in the shorter subjective duration of the SAME than DIFF stimuli.

**Discussion**

In the present study, we investigated how the changes in subjective duration are related to their temporal profiles of neural activation in sensory areas. Stimulus repetition in the SAME trials induced neural adaptation in the higher visual areas and reduced both peak amplitude and latency of neural activity. Although this reduction in peak latency produced a selective increase in the onset-offset interval of the test stimulus in the SAME trials, we found that the test in SAME was judged to be shorter than that in DIFF. Instead, a comparison of visual neural activity between long and short trials (Fig. 5) revealed that the stimulus eliciting stronger neural activity tended to be perceived as longer, regardless of the onset-offset interval. This result indicates a close relationship between the strength of neural activity and subjective duration and provides an answer as to why the test was perceived to be shorter in SAME trials than in DIFF trials: the reduction of peak amplitude in the test stimulus of SAME trials (by neural adaptation) shortened the subjective time interval of that stimulus.

**Does the Shortening of Onset Peak Latency Mean an Acceleration of Recognition Speed?**

Figure 4 shows the dissociation between the relative time scales of subjective (% long) and neural (onset-offset interval) indices. The starting point of recognition of the test stimulus was selectively shortened for SAME trials by the neural adaptation, resulting in an extension of the onset-offset interval of that stimulus, regardless of the fact that the same stimulus was perceived as shorter than the test stimulus in DIFF trials. This conclusion is, however, based on an assumption that the neural adaptation facilitated the “recognition speed itself” of the repeated stimulus. If the shortening of peak latency does not necessarily involve the acceleration of stimulus recognition, the conclusion above is questionable. Does the shortening of onset peak latency mean an acceleration of recognition speed?

Overall, the results in previous studies imply an affirmative answer to this question. As reviewed by Henson (2003), a close relationship has been indicated between neural adaptation and the psychological priming effect (the reduction in reaction time of a repeatedly presented stimulus), although some differences between them were pointed out. Also, our previous MEG study using a priming paradigm (Noguchi and others 2004) provided evidence that the reduction in the peak latency of the 300-ms neuromagnetic response was implicated in the acceleration of recognition of the presented stimuli. In this study, 2 visual patterns (alphabetic letters) made by the RDB method were displayed sequentially. The 1st and 2nd letters were either the same (e.g., A → A, SAME trials) or different (A → B, DIFF trials), and subjects were required to judge whether the 2nd stimulus was a vowel or consonant. As in many psychological studies, this task produced a priming effect, and the reaction time of button
press became significantly smaller in SAME than DIFF trials. Accordingly, the peak latency of the 300-ms higher visual responses to the 2nd stimulus was also selectively shortened for SAME trials, and we further found a significant correlation between these reductions in peak latency and in the behavioral reaction time. These results indicated that the shortening of onset peak latency of the 300-ms component observed in both previous and present studies reflected the reduction in recognition speed of the presented stimulus.

**Involvement of the Early Visual Cortex in Shaping Temporal Representation**

One alternative explanation for the dissociation of onset–offset intervals and subjective duration is that the subjects made up their time sensations using temporal information in other sensory areas such as early (not high level) visual regions. Because the shape processing of visual stimuli is not necessary in our task, subjects might perform the task by measuring the timing when their early visual areas (e.g., V1) detect the appearance or disappearance of edges of any stimuli. Several aspects of our data, however, indicate that this was not the case in the present study. First, we obtained similar results of % long both in behavioral and MEG sessions (the test stimulus in the SAME trials was always judged to be shorter than that in the DIFF trials, Fig. 1B). As described in Materials and Methods, the visual patterns (< and >) in the behavioral session were defined by the difference in luminance from the background (1st-order cue), whereas those in the MEG session were defined by

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**Figure 6.** Slow buildup activity in the SMA. (A) Averaged waveforms across 24 MEG sensors over the frontocentral region. The grand-averaged responses to the 600-ms test stimulus in SAME (thin lines) and DIFF (thick lines) trials are shown. The positions of the 24 sensors are indicated by the dotted line in Figure 2A. (B) Source location of the buildup activity. Left panel shows a contour map of magnetic field patterns (solid lines: outflux, broken lines: influx) in a representative subject at a latency of 512 ms. The arrow indicates a direction of the estimated current flow. Mean dipole locations across 7 subjects were 5 ± 1.5, 40 ± 3.7, 99 ± 4.4 and shown on the anatomical images of 1 subject in the right panels. (C) Mean amplitudes of buildup waveforms 450–550 ms after the stimulus onset (shaded area in A). Errors bars denote the standard error across 13 subjects. The SAME trials (blank bars) showed significantly smaller mean amplitudes than the DIFF trials (filled bars). (D) A correlation in neural activity changes (DIFF–SAME) between VEF peak amplitude (Fig. 4B, lower right panel) and SMA mean activity (Fig. 6C). The significant correlation of these 2 indices suggests strong connectivity between the higher visual areas and the SMA region. *P < 0.05, significance test for correlation coefficients.
a nonluminance cue (static-dynamic segregation of random dots, 2nd-order cue). The essentially identical results in both sessions thus imply that our subjects conducted the duration discrimination task by recruiting the cue-invariant cells in high-level visual areas (Sary and others 1993; Zeki and others 2003), rather than the luminance-sensitive early visual cells in V1 or V2. Second, several previous studies have shown that the early visual areas such as V1 are not sensitive to the neural adaptation effect induced by the stimulus shape congruency, whereas this effect is reliably observed in high-level visual areas (Buckner and others 1998; Boynton and Finney 2003). These findings suggest that, although we reported a neural adaptation effect in the higher visual regions (reduction in peak amplitude and latency, Fig. 4), activities in early visual areas were not changed in the present study. Therefore, if subjects did the task based on the temporal information in early visual areas, no changes in subjective duration should be expected between SAME and DIFF, which is not the case as shown in Figure 1B.

**Frontocentral Buildup Waveform and Contingent Negative Variation**

In the present study, we observed slow buildup activity from the frontocentral regions during the discrimination task. Although these waveforms were similar to the contingent negative variation (CNV) reported in previous EEG studies (Macar and others 1999; Pfeuty and others 2003), one would argue that there are some qualitative differences. First, the buildup activity in the present study was a neuremagnetic response measured with MEG, whereas almost all studies on CNV have used EEG. Because the MEG sensors used in the current study (planar-type gradiometers) become less sensitive to neural activity in deeper regions of the brain, the cortical areas contributing to the climbing waveforms might differ between previous and present studies. The dipole analysis in Figure 6B, however, indicated that, in more than half of 13 subjects, a reliable signal source could be estimated in the SMA, the same location as in previous EEG studies. This result was consistent with previous studies reporting sensitivity of MEG to neural responses from the SMA (Erdler and others 2000; Huang and others 2004). A theoretical study using a Monte-Carlo analysis has also supported the possibility that MEG could detect activity in the medial wall, such as the SMA and premotor area (Hillebrand and Barnes 2002). Thus, the MEG buildup activity and previous CNV are thought to be generated from at least similar, if not identical, areas in superior medial regions.

Another possible difference between present and previous studies is a time range of stimulus used in the experiments. The current experiment used standard and test stimuli of less than 1 s, whereas the modulation of CNV has been mostly observed in a task with durations of several seconds. Given that some previous studies pointed out the separation of temporal processing in sub- and suprasecond ranges (Lewis and Miall 2003b; Mauk and Buonomano 2004), this difference in stimulus duration might make difficult direct comparison between CNV and the present buildup activity. However, whereas most previous EEG studies have used a stimulus of longer than 1 s, several studies reported robust CNV waveforms in subsecond periods (e.g., Pfeuty and others 2003), the same time range as the present study. In addition, recent functional magnetic resonance imaging studies have reported significant activity of the SMA in the processing of subsecond intervals (Ferrandez and others 2003), and, indeed, there is a study showing the involvement of the SMA during measurement of both sub- and suprasecond ranges (Lewis and Miall 2003a). These studies suggest that the buildup activity from around the SMA is essentially the same regardless of whether the stimulus is shorter or longer than 1 s. We therefore concluded that the buildup activity in the present study can be compared with CNV in previous studies. Some differences, however, should be noted for the interpretation of our data, such as the relatively high cutoff frequency of the high-pass filter (0.1 Hz) in the present study.

**Relationship of the Higher Visual Cortex with Temporal Processing Network in the Brain**

Previous neurophysiological and neuroimaging studies have investigated where in the human brain the central system for time processing is located. Mainly by comparing the brain activation during temporal and nontemporal tasks, these studies have found that temporal information is selectively processed in an extensive network of regions, including the basal ganglia (Schubotz and others 2000; Rao and others 2001; Belin and others 2002; Ferrandez and others 2003; Coull and others 2004), SMA (Macar and others 1999; Schubotz and others 2000; Ferrandez and others 2003; Lewis and Miall 2003a; Coull and others 2004), lateral prefrontal cortex (Maquet and others 1996; Harrington and others 1998; Rubia and others 1998; Pouthas and others 2000; Onoe and others 2001; Rao and others 2001; Belin and others 2002; Ferrandez and others 2003; Smith and others 2003; Lewis and Miall 2003a; Coull and others 2004), intraparietal regions (Maquet and others 1996; Harrington and others 1998; Schubotz and others 2000; Rao and others 2001; Belin and others 2002; Ferrandez and others 2003; Leon and Shadlen 2003; Lewis and Miall 2003a; Coull and others 2004), and cerebellum (Jueptner and others 1995; Maquet and others 1996; Schubotz and others 2000; Tracy and others 2000; Rao and others 2001; Belin and others 2002). Although it is controversial whether a neural system specialized for time processing in the millisecond range exists or not (Ivry and Spencer 2004; Mauk and Buonomano 2004), this corticostriatal–thalamic loop is presently thought to play an important role in time perception of humans and animals. The current results in higher visual areas thus indicate that both temporal and nontemporal (i.e., neural intensity) information of visual responses can affect the temporal processing in this central network of the internal clock. Indeed, we showed that the activation in the SMA, a potential candidate for a temporal accumulator, is closely correlated with the changes in intensity of the higher visual responses (Fig. 6). One should note, however, that the present study did not investigate subcortical brain regions related to time perception, such as the striatum or substantia nigra (Matell and Meck 2004).

Overall, the present results suggested a possible strategy used by our clock system to convert sensory information into time representation. Although further investigation of internal clock mechanisms is necessary, the present study provides useful information for future studies to reveal the fundamental time concepts of humans.

**Notes**

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