Differential Priming Effects of Color-Opponent Subliminal Stimulation on Visual Magnetic Responses

Minoru Hoshiyama,^{1,2*} Ryusuke Kakigi,^{1,3,4} Yasuyuki Takeshima,¹
Kensaku Miki,¹ and Shoko Watanabe^{1,3,4}

¹Department of Integrative Physiology, National Institute for Physiological Sciences, Myodaiji, Okazaki, Japan

²Department of Health Sciences, Faculty of Medicine, Nagoya University, Higashi-ku, Nagoya, Japan

³Department of Physiological Sciences, School of Life Sciences, The Graduate University for Advanced Studies, Hayama, Kanagawa, Japan

⁴RISTEX, Japan Science and Technology Agency, Tokyo, Japan

Abstract: We investigated the effects of subliminal stimulation on visible stimulation to demonstrate the priority of facial discrimination processing, using a unique, indiscernible, color-opponent subliminal (COS) stimulation. We recorded event-related magnetic cortical fields (ERF) by magnetoencephalography (MEG) after the presentation of a face or flower stimulus with COS conditioning using a face, flower, random pattern, and blank. The COS stimulation enhanced the response to visible stimulation when the figure in the COS stimulation was identical to the target visible stimulus, but more so for the face than for the flower stimulus. The ERF component modulated by the COS stimulation was estimated to be located in the ventral temporal cortex. We speculated that the enhancement was caused by an interaction of the responses after subthreshold stimulation by the COS stimulation and the suprathreshold stimulation after target stimulation, such as in the processing for categorization or discrimination. We also speculated that the face was processed with priority at the level of the ventral temporal cortex during visual processing outside of consciousness. *Hum Brain Mapp* 27:811–818, 2006. © 2006 Wiley-Liss, Inc.

Key words: face; MEG; ERP; subliminal; priming; human

INTRODUCTION

In the field of cognitive neuroscience, visual stimulation below the threshold for awareness causes cognitive or behavioral changes to subsequent stimulation [Smith et al.,

1959; Somekh and Wilding, 1973]. Recently, the effects of stimulation below such a threshold (subliminal stimulation) on visual processing have been investigated for the processing of words [Dehaene et al., 2001; Luo et al., 2004] and facial emotion [Liddell et al., 2004; Morris et al., 1998; Williams et al., 2004]. The latter studies showed that facial emotion processing was initiated without conscious awareness and was modulated by subliminal stimulation as well as by supraconscious stimulation. In the processing of facial emotion, the information from the figure of a face or facial components for emotional expression should be processed at the same time as or before the emotional information. We considered that the face was processed at the initial stage of visual processing, e.g., categorization or discrimination, automatically outside of consciousness, and we reported pre-

*Correspondence to: Minoru Hoshiyama, MD, PhD, Department of Health Sciences, Faculty of Medicine, Nagoya University, Daiko-Minami, Higashi-Ku, Nagoya, 444-8585 Japan.
E-mail: hoshiyama@met.nagoya-u.ac.jp

Received for publication 31 May 2005; Accepted 30 September 2005

DOI: 10.1002/hbm.20222

Published online 1 March 2006 in Wiley InterScience (www.interscience.wiley.com).

viously that subconscious stimulation by a face evoked a larger response than that with other figures in the ventral temporal (VT) areas, using electroencephalography (EEG) and magnetoencephalography [MEG; Hoshiyama et al., 2003].

In recent studies, including our own study, subconscious stimulation was presented using the backward masking effect on a briefly presented stimulation by a following stimulation [Dehaene et al., 2001; Hoshiyama et al., 2003; Liddell et al., 2004; Luo et al., 2004; Morris et al., 1998; Noguchi and Kakigi, 2005; Williams et al., 2004]. The masked stimulus, however, was actually perceived only when the target stimulus was presented. Backward masking is a key experimental paradigm with which to investigate neural processing during consciousness, but we considered that actual subconscious or subdiscrimination-threshold stimulation might be more effective for investigating the visual processes outside of consciousness.

In the present study, we used a novel method of subliminal stimulation, a continuous but indiscernible stimulation of a figure. We described this subliminal stimulation as a color-opponent subliminal (COS) stimulation. The COS stimulation was not the conventional masked stimulation used in previous studies of subliminal stimulation, but rather a stimulation related to the color-opponent visual process [Schiller and Logothetis, 1990]. We modified the conventional color-opponent flicker stimulation to be controlled by a personal computer, and the figural content of the stimulus could not be discerned during the COS stimulation. Using this stimulation, we investigated the effect of subliminal stimulation on visible stimulation in the inferior temporal region, which is responsible for object discrimination. We showed the priority of face perception in the visual processes outside of consciousness in the present study.

SUBJECTS AND METHODS

Subjects

Eleven healthy adult volunteers (6 men, 5 women; age range 28–40 years) with no history of neurological disease were studied. Informed consent to participate in the study, which was approved by the Ethics Committee of the National Institute for Physiological Sciences, Okazaki, Japan, was obtained from all subjects before the study. The visual acuity of the subjects was controlled at 1.0 or higher with contact lenses during the experiment.

Color-Opponent Stimulation

Four reciprocal pairs of figures in color (face, flower, random pattern, and blank) were presented alternately (Fig. 1) at high frequency (100 Hz) during the COS conditioning stimulation period. One figure was drawn in red on the background, which was a red and green checkerboard pattern with black mesh, and the other was drawn in green on the background, in which the red and green pixels were alternately changed (Fig. 1). We made figures with red-

Figure 1.

Pairs of figures. Face, flower, random pattern, and blank were drawn with a red and green checkerboard with a black mesh. Expanded parts of figures are shown at the top of the figure. Each pair was colored alternately (R and G). During the interstimulus interval, another random pattern (Interval) was presented. At the center of the figure, a fixation point was provided in blue. The color-opponent subliminal (COS) stimulation was produced by presenting a pair of figures alternately (red–green–red–green–...) at 100 Hz (10-ms duration for each stimulation). The blank figures were used as a control COS stimulation.

green-blue (RGB) in 256 bits on the computer, and the green and red were colored by (R, G, B: 255, 0, 0) and (0, 255, 0), respectively. We used actual colors on a display screen with a photometer (CS-100; Konica-Minolta Co., Japan), and the color on the Commission Internationale de l'Éclairage (CIE) coordinate for red and green was (luminance, x , y : 17.3, 0.585, 0.360) and (51.7, 0.306, 0.570), respectively. All stimulations were controlled by a personal computer with a dis-

play monitor (GDM-F250; Sony, Japan), which was placed outside of a magnetically shielded room. The figures were presented through a window on a wall of the shielded room, and the distance from the subject's face to the monitor's screen was 2 m. The size of the figure presented was 240×240 pixels (140×140 mm on the monitor; 4 degrees in the visual field), and the size of the mesh was 1 pixel square (0.016 degrees). At the center of the screen, there was a fixation point in blue (2×2 pixels).

By presenting a pair of figures alternately (red–green–red–green–...) at 100 Hz (10 ms presentation for each stimulation), the figure was completely subliminal and the subjects only saw a yellow square during the alternate presentation period. The accuracy of the presentation frequency and timing was confirmed independently using an oscilloscope. The mean luminance of the figure presented during the COS and target period was 17.2 ± 0.5 (mean $\pm$ SD, cd/m^2) and 17.1 ± 0.4 , respectively, and the value of the CIE coordinate of the background during the COS stimulation was (x , y : 0.406, 0.487).

The theoretical basis of the present method for subliminal stimulation was based on the visual processing mediated by the color-opponent and broadband systems [Barbur et al., 1999; Derrington et al., 1984; Schiller and Logothetis, 1990; Wiesel and Hubel, 1966]. Both systems contribute to visual perception at a low temporal frequency of visual stimulation, but at high temporal rates for visual stimulation, the process for the color-opponent system is limited [Schiller and Logothetis, 1990]. When iso-luminant red and green colors were alternately flickered, the colors fused, and the objects drowned in the colors therefore were not perceived but a yellow flickering stimulus was recognized [Barbur et al., 1999; Schiller and Logothetis, 1990].

We modified the basic method of flicker stimulation. One advantage of our stimulus method was using a black mesh over the figure. In the conventional method of color-opponent stimulation without a black mesh, red and green in the figure should be strictly iso-luminant to each other to cause a yellowish flicker; however, in practice it is difficult to control the two colors to be iso-luminant on a monitor screen. To solve this problem we covered the figure drowned by pixels with a black mesh, which prevented one color from directly being adjacent to the other color. With a black mesh the edge caused by the differences in luminance between two colors during COS stimulation was not produced; therefore, we did not need to strictly control the two colors for them to be iso-luminant during COS stimulation.

The advantages of this stimulation method are that subliminal stimulation can be presented as long as the experiment requires and that the parameters of the visual stimulation, i.e., luminance and contrast, are constant during the stimulation period.

Experimental Protocol

One epoch of visual stimulation comprised the presentation of the alternative COS conditioning stimulation for 1 s, and one of the figures (target figure) was presented 0.5 s

Figure 2.

Experimental design. A pair of figures in Figure 1 was presented alternately at 100 Hz for 1.0 s as the color-opponent subliminal (COS) conditioning stimulation followed by the presentation of a figure for 0.5 s (Target). During the interstimulus interval, a large stable random pattern was presented (Interval). The MEG signals were collected from 0.1 s before the onset of the target stimulation to 0.5 s after the onset.

after the COS stimulation (Fig. 2). The trigger to record the brain response was the onset of the target figure. The inter-epoch interval was random between 2–3 s and another random pattern (Interval in Fig. 1) was presented during the period. A face, a flower, a random pattern, and a blank pattern were presented for the COS figures, and a face and a flower were used for the target figures. For each target stimulus, a red or green figure was presented randomly, and the last figure during the COS stimulation was a figure of the opposite color to that of the target figure. We measured the stimulation directly from the display by a photosensor and checked that the COS and target stimulations were precisely displayed. The combination of COS and target figures therefore gave eight patterns, and the combinations were arranged randomly in an epoch. One recording consisted of 90 epochs for each combination; thus, 720 epochs were presented in one recording. One recording was divided into six sessions with short intervals for the subjects to rest.

MEG and Event-Related Cortical Magnetic Field Recording

We used 204-channel planar-type gradiometers (Vector View; Elekta Neuromag; Helsinki, Finland) for recording MEG, with a bandpass filter of 0.1–50 Hz and digitized the data at a sampling rate of 998 Hz. The period from 100 ms before to 500 ms after the target stimulus onset was recorded for an epoch (Fig. 2). The baseline was offset using a period from 100 ms to 10 ms before the stimulus for the analysis. Rejecting epochs with a signal larger than 3pT, 90 epochs for each COS conditioning and target stimulation were collected and averaged separately. For each averaged signal, 52 chan-

Figure 3.

Waveforms of event-related cortical magnetic fields. Fifty-two planar type coils were selected for the dipole analysis in the right temporal (solid circle) and occipital areas (dashed circle). The RMS curves shown in the middle of the figure were calculated from each group of selected coils to determine the peak of each component. Changes in ERF waveforms, recorded from two representative subjects, after the onset of target stimulation at sensors A (1M) and B (2M) are presented at the bottom. The 2M changed with each combination of the COS conditioning stimula-

tion (F, Face; T, Flower [tulip]; R, Random dots; B, Blank [Control]), whereas the 1M did not. For example, T-F means that the tulip was shown in the COS period and the face was shown in the target period. Another deflection was obtained in RMS and sensor A (*) at approximately 200 ms after the stimulus. For this component, the RMS and estimated current were not different among conditions, and the contour map and source localization were not consistent (see text).

nels were selected in each occipital and right temporal area and the root mean square (RMS) of the magnetic field was calculated (Fig. 3) to determine the peak latency of the event-related cortical magnetic field (ERF) components. In 9 of 11 subjects, the 2M response was obtained dominantly in the right hemisphere, and the remaining two showed bilateral responses. For the 2M response, the dipole and moment were estimated using selected sensors in the right temporal area. At the peak latency of RMS, dipole location and moment (in nAm) were estimated. We estimated the

dipole at the peak latency of 1M and 2M, when the isomagnetic field pattern was consistent around the peak latency at 5 points of sampling before and after the peak latency (approximately 10 ms around the peak latency). To compare the effect of the COS conditioning stimulation, the dipole moment for the ERF components was estimated after face or flower target stimulation preceded by the COS stimulation. The dipole moment values were standardized by dividing them by those after COS stimulation with blank figures (control COS condition), because the dipole moment

for face target stimulation was larger than that for flower stimulation, even in the control condition.

The standardized values were compared after log transformation using one-way repeated-measures analysis of variance (ANOVA) and the Tukey-Kramer multiple comparison test.

Source Analysis and Overlaying On Magnetic Resonance Images

The single current dipole model was used to estimate the locations of the cortical activities that produced the magnetic fields [Sarvas, 1987]. The equivalent current dipole (ECD) at the peak of each ERF component was estimated from the magnetic signals obtained from 52 selected channels in the right hemisphere (Fig. 3).

Magnetic resonance (MR) imaging scans (150XT 1.5T; Shimadzu, Kyoto, Japan) were obtained from all subjects. T1-weighted coronal and axial images obtained every 1.5 mm were used for superimposition of the MEG source localizations. The same anatomical landmarks used to create the MEG head-based 3-D coordinate system, i.e., bilateral preauricular points and nasion, were visualized in the MR images by affixing to these points high-contrast cod liver oil capsules (3 mm in diameter). The MEG and MR imaging (MRI) anatomical landmarks allowed the transformation of the head-based 3-D coordinate system used for MEG source analysis into coordinates for the MR images.

RESULTS

A behavioral test was run before and immediately after the experiment, and it was checked that the COS stimulation was indiscernible (100%) to all participants. All subjects reported that the figural content of the stimulus could not be discerned but a yellow-colored rectangle appeared during the COS period.

The ERF after target stimuli showed two major deflections of the RMS, curve of selected channels at 120.2 ± 22.8 ms (1M, mean $\pm$ SD) and 220.8 ± 22.5 ms (2M; Fig. 3).

The estimated moment for 2M was affected significantly by the COS stimulation in the face ($P < 0.01$, ANOVA) and in the flower ($P < 0.02$) sequences. The moment for the F-F condition was significantly larger than that for B-F, but the values for other conditions did not differ from that of the control. In the control COS condition, the estimated moment for 2M for the face was significantly larger (37.7 ± 24.7 nAm) than that for the flower (31.5 ± 16.6 nAm; $P < 0.02$). The estimated moment for 1M did not differ among the conditions, and there was no difference in 1M moment in the control COS condition (flower, 12.0 ± 6.0 nAm; face, 12.2 ± 6.6 nAm).

The estimated dipole moment for the 1M standardized to the control COS conditioning stimulus did not differ among the COS conditioning stimuli (Fig. 4). The standardized moment for 2M, however, significantly differed among the COS conditioning stimuli ($P < 0.01$; Fig. 4). When the figure during the COS stimulation was the same as the target

Figure 4.

Estimated currents ($|Q|$) of the dipoles for 1M and 2M for each COS conditioning and target combination (F, Face; T, Flower [tulip]; R, Random dots). Values were standardized to the estimated current when a blank pattern (Control) was presented during the COS period in a logarithmic vertical axis. For example, T-F means that the tulip was shown in the COS period and the face was shown in the target period. The estimated current was significantly altered by the subliminally presented figure ($P < 0.01$, ANOVA). The estimated current was largest when the face was presented during the COS and target periods (** $P < 0.03$, Tukey-Kramer test). For the flower stimulus as the target, the value was larger when the flower was shown during the COS period than when the face was shown (* $P < 0.05$). There was no difference in the current for 1M.

stimulus, the dipole moment was larger than that when different figures were presented in the COS and target stimulations ($P < 0.05$). In addition, when the face was presented during the COS conditioning, the dipole moment after the target face stimulation was much larger than those for other combinations of COS conditioning and target stimuli ($P < 0.03$).

The iso-magnetic contour maps of 1M and 2M showed a one-dipole pattern on the scalp in the occipital area and the right temporal area, respectively (Fig. 3), and the estimated dipoles for 1M and 2M were located around the occipital pole of the calcarine fissure, which was possibly the primary visual cortex (V1; goodness of fit [GOF] between the recorded magnetic field and the values expected from the ECD model: $78.5\% \pm 11.8\%$, 95% dipole position confidence volume [95% CV]: 509.8 ± 286.3 mm³) and in the ventral temporal (VT) areas (GOF: $86.3\% \pm 3.67\%$, 95% CV: 757.9

Figure 5.

The dipole locations for two subjects on MR images. The subjects were the same ones as in Figure 3. The dipole for 1M after target face stimulation was estimated to be located in the primary visual cortex (left), and the dipole for 2M was estimated to be in the inferior temporal area of the right hemisphere (right). The dipole location did not differ among the three COS conditions in both subjects (o: Face, Tulip, and Random dots).

$\pm 521.8 \text{ mm}^3$), respectively (Fig. 5). There was no difference in the position of the dipole among the COS conditioning stimuli.

Another deflection of RMS was obtained in the occipital set of sensors, whose peak latency was $206.9 \pm 59.8 \text{ ms}$ after the stimulation (Fig. 3). The estimated current for the component was not different among conditions, and the dipole was not estimated in a consistent area of the brain.

DISCUSSION

Three major findings obtained for the present study were: (1) COS stimulation affected the response after visible stimulation; (2) COS stimulation enhanced the response after visible stimulation when the figures in the COS and visible stimulations were similar; and (3) the facilitating effect of the COS stimulation was greater with the figure of the face than with that of the flower.

The initial finding showed evidence that subliminal stimulation by color-opponent flicker stimulation modified the brain response without awareness. This finding supports the results of a previous study of subliminal stimulation [Kihlstrom, 1987]. In early studies of subliminal stimulation, researchers assumed that perception was associated with an absolute threshold, represented by the weakest detectable stimulus. However, the probability of detection was related directly to the stimulus intensity, even below the detection threshold, suggesting that the subdetection threshold stimulation was still processed by the sensory perceptual system [Kihlstrom, 1987]. As for recent studies of unconscious priming, subliminal stimulation by masked stimulation had a repetition-related decrement of response for the subsequent supraconscious stimulation, at least in some fundamental facial emotional processes [Liddell et al., 2004; Morris et al., 1998; Williams et al., 2004].

In the present study, the facilitating effects of the COS stimulation on the 2M response were evident for both the face and flower target stimuli, and the effect of the COS conditioning stimulation was greater for the response to the face than to the flower. Whether the prime stimulation is presented consciously or unconsciously, repetition priming has been characterized neurophysiologically as a decreased response after stimulus repetition [Desimone, 1996; Noguchi et al., 2004; Wiggs and Martin, 1998]. Henson et al. [2000] recently reported enhancement of the priming-related response in the VT area for unfamiliar stimuli, however, and their result indicated that the priming-related effect was not unitary.

In previous studies of subliminal stimulation [Dehaene et al., 1998, 2001; Hoshiyama et al., 2003; Liddell et al., 2004; Morris et al., 1998; Williams et al., 2004], the presentation period of the stimulation was 16–20 ms or less, but the stimulation was definitely visible without masking stimulation preceding the target stimulation to be masked. Because the COS stimulation in the present study consisted of the rapid alternation of red/green stimuli, each of which were 10 ms in duration, we suspect that the amount of visual signal received by subjects was less than that in experiments using masked stimulation. Henson et al. [2000] reported that a figure unfamiliar to the subject evoked an increased response with repetition of the stimulation. The figures used in the present study were quite simple, however, and they became familiar to the subjects after presentation a few times. Unfamiliarity is thus not likely to be the reason for the enhancement of response, and we proposed another possibility for the priming effect of the subliminal stimulation.

We speculated that the facilitation of the target response was caused by a temporal summation of the sub- and suprathreshold stimulation, when the preceding stimulation was subthreshold at a level of visual processing. A temporal summation of subthreshold stimulation was observed at the cellular level in the central nervous system [Nettleton and Spain, 2000], but it has not been observed in a noninvasive study of the human central nervous system. One major reason is that the actual threshold of neural activity in the central nervous system can not be determined, because the intensity or amount of stimulation has been determined based on the subject's conscious perception. It was considered that the parvocellular layer of the lateral geniculate nucleus (LGN) was responsive to the color-opponent system [Schiller and Logothetis, 1990], but on the other side, the magnocellular pathway responds better to higher temporal frequencies and also responds to chromatic modulation [Schiller and Malpeli, 1977]. In addition, Purpura et al. [1988] showed that magnocellular cells have better contrast gain and are more responsive to the processing of fine patterns than are parvocellular cells in primates. Magnocellular lesions at the LGN level produced both monochromatic and heterochromatic flicker at high frequency [Schiller and Logothetis, 1990]. COS stimulation therefore likely affected both parvo- and magnocellular systems by using alternating red and green stimuli and high-frequency flicker, and caused a subthreshold stimulation possibly at the level of the LGN or later stages of the visual system such as V4 and VT. We considered that the strength of signals to the visual cortices during the COS stimulation was different from that of the masking subconscious stimulation in which signals evoked by the masked stimulation were suprathreshold at the level of the LGN. The strength of the signal for the conditioning stimulation at the LGN and cortical levels might determine the priming effect, i.e., a facilitation or suppression effect.

In the occipital area, we obtained a small response (1M) and there was no significant difference among the conditions. Another component was recognized in the occipital area at a latency of around 200 ms. There may be three possibilities for this component: (1) a second response after the initial response in V1; (2) spreading response of 2M in the VT area; and (3) summation of both (1) and (2) responses. Because the dipole was not estimated consistently, we considered that the component was recorded because of the second or third reason. We could not exclude the possibility that the priming process also occurred around V1 in the present study. Because the COS and target stimulations were nearly iso-luminant, the response in V1 was small, which could be a reason why we could not observe differences among the conditions.

Although we could not confirm the mechanism for the enhancement of the response by COS stimulation, the effect was evident for the face stimulus. The brain responses after illustrative face figures might not be identical to those for real photographs, although we found the equivalent dipole for the face figure in a similar region for a real face. Previous

literature, however, reported the physiological significance of the illustrative face [Botzel and Grusser, 1989], which suggested that the significance of an illustrative face could be analogous to that of a photographed face. In addition, the latency of 2M was approximately 220 ms after the stimulation, which was slightly longer than that for the facial response in the VT area in previous studies, which was 150–200 ms [Allison et al., 1994; Watanabe et al., 1999, 2005]. We considered that this delay in peak latency could be due to differences in the figure presented. The modulation of the response by the COS stimulation occurred in the estimated dipole moment of 2M located in the VT area (Fig. 4). The face-sensitive regions have been reported in the VT area in humans [Allison et al., 1994; Puce et al., 1995; Watanabe et al., 1999, 2005], although these regions were distributed widely and overlapped with those of other objects [Haxby et al., 2001]. The VT region was used for the categorization of visual information and the ERP component peaking at 170–200 ms after the visual stimulation (N170 or N200), which corresponded to 2M in the present study, reflected the categorization process [Allison et al., 2002]. We considered that indiscernible stimulation, i.e., the COS stimulation, in the present study might have led to subthreshold signals in the VT regions and that sub- and suprathreshold interaction, which was different from the repetition-related inhibitory priming effect, occurred in that region.

In conclusion, the COS stimulation enhanced the response to visible stimulation, different from the repetition-related inhibitory priming effect, more evidently for the face stimulus than the non-face (flower) stimulus. We considered that the face was processed with priority, even in the process for subliminal stimulation.

REFERENCES

- Allison T, Ginter H, McCarthy G, Nobre AC, Puce A, Luby M, Spencer DD (1994): Face recognition in human extrastriate cortex. *J Neurophysiol* 71:821–825.
- Allison T, Puce A, McCarthy G (2002): Category-sensitive excitatory and inhibitory processes in human extrastriate cortex. *J Neurophysiol* 88:2864–2868.
- Barbur JL, Weiskrantz L, Harlow JA (1999): The unseen color aftereffect of an unseen stimulus: insight from blindsight into mechanisms of color afterimages. *Proc Natl Acad Sci USA* 96:11637–11641.
- Botzel K, Grusser OJ (1989): Electric brain potentials evoked by pictures of faces and non-faces: a search for “face-specific” EEG-potentials. *Exp Brain Res* 77:349–360.
- Dehaene S, Naccache L, Cohen L, Bihan DL, Mangin JF, Poline JB, Riviere D (2001): Cerebral mechanisms of word masking and unconscious repetition priming. *Nat Neurosci* 4:752–758.
- Dehaene S, Naccache L, Le Clec’h G, Koechlin E, Mueller M, Dehaene-Lambertz G, van de Moortele PF, Le Bihan D (1998): Imaging unconscious semantic priming. *Nature* 395:597–600.
- Derrington AM, Krauskopf J, Lennie P (1984): Chromatic mechanisms in lateral geniculate nucleus of macaque. *J Physiol* 357: 241–265.

- Desimone R (1996): Neural mechanisms for visual memory and their role in attention. *Proc Natl Acad Sci USA* 93:13494–13499.
- Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P (2001): Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293:2425–2430.
- Henson R, Shallice T, Dolan R (2000): Neuroimaging evidence for dissociable forms of repetition priming. *Science* 287:1269–1272.
- Hoshiyama M, Kakigi R, Watanabe S, Miki K, Takeshima Y (2003): Brain responses for the subconscious recognition of faces. *Neurosci Res* 46:435–442.
- Kihlstrom JF (1987): The cognitive unconscious. *Science* 237:1445–1452.
- Liddell BJ, Williams LM, Rathjen J, Shevrin H, Gordon E (2004): A temporal dissociation of subliminal versus supraliminal fear perception: an event-related potential study. *J Cogn Neurosci* 16:479–486.
- Luo Q, Peng D, Jin Z, Xu D, Xiao L, Ding G (2004): Emotional valence of words modulates the subliminal repetition priming effect in the left fusiform gyrus: an event-related fMRI study. *Neuroimage* 21:414–421.
- Morris JS, Ohman A, Dolan RJ (1998): Conscious and unconscious emotional learning in the human amygdala. *Nature* 393:467–470.
- Nettleton JS, Spain WJ (2000): Linear to supralinear summation of AMPA-mediated EPSPs in neocortical pyramidal neurons. *J Neurophysiol* 83:3310–3322.
- Noguchi Y, Inui K, Kakigi R (2004): Temporal dynamics of neural adaptation effect in the human visual ventral stream. *J Neurosci* 24:6283–6290.
- Noguchi Y, Kakigi R (2005): Neural mechanisms of visual backward masking revealed by high temporal resolution imaging of human brain. *Neuroimage* 27:178–187.
- Puce A, Allison T, Gore JC, McCarthy G (1995): Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J Neurophysiol* 74:1192–1199.
- Purpura K, Kaplan E, Shapley RM. (1988): Background light and the contrast gain of primate P and M retinal ganglion cells. *Proc Natl Acad Sci USA* 85:4534–4537.
- Sarvas J (1987): Basic mathematical and electromagnetic concepts of the biomagnetic inverse problem. *Phys Med Biol* 32:11–22.
- Schiller PH, Logothetis NK (1990): The color-opponent and broadband channels of the primate visual system. *Trends Neurosci* 13:392–398.
- Schiller PH, Malpeli JG (1977): Properties and tectal projections of monkey retinal ganglion cells. *J Neurophysiol* 40:428–445.
- Smith GJ, Spence DP, Klein GS (1959): Subliminal effects of verbal stimuli. *J Abnorm Soc Psychol* 59:167–176.
- Somekh DE, Wilding JM (1973): Perception without awareness in a dichoptic viewing situation. *Br J Psychol* 64:339–349.
- Watanabe S, Kakigi R, Koyama S, Kirino E (1999): Human face perception traced by magneto- and electro-encephalography. *Brain Res Cogn Brain Res* 8:125–142.
- Watanabe S, Miki K, Kakigi R (2005): Mechanisms of face perception in humans: a magneto- and electro-encephalographic study. *Neuropathology* 25:8–20.
- Wiesel TN, Hubel DH (1966): Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *J Neurophysiol* 29:1115–1156.
- Wiggs CL, Martin A (1998): Properties and mechanisms of perceptual priming. *Curr Opin Neurobiol* 8:227–233.
- Williams LM, Liddell BJ, Rathjen J, Brown KJ, Gray J, Phillips M, Young A, Gordon E (2004): Mapping the time course of nonconscious and conscious perception of fear: an integration of central and peripheral measures. *Hum Brain Mapp* 21:64–74.