

Sexual Influence on Gaze-Guided Social Attention

Etsuro Hori^{1,2}, Masahiko Tsunoda^{2,3}, Miho Takeshima^{1,2}, Michio Suzuki^{2,3}, Masayoshi Kurachi^{2,3}, Taketoshi Ono^{1,2} and Hisao Nishijo^{1,2}*

ABSTRACT

Although sexual influence on various cognitive functions has been reported, sexual influence on gaze-guided social attention remains unknown. To investigate an influence of sex of facial stimuli on gaze-guided social attention, a modified Posner's paradigm was applied to female and male subjects. In the task, a female or male facial stimulus gazing toward the right or left side was presented at the center of a display. After variable delay from onset of the facial stimulus, a target appeared on the left or right side of the display, and the reaction time for target detection was recorded. Statistical analyses of reaction time by the analysis of variance (ANOVA) revealed that a significant main effect of congruity between gaze direction and target location, and significant interactions among congruity, sex of facial models and sex of the subjects. When the female facial cues were presented, reaction time was significantly shorter in the congruent trials in the male but not female subjects. When the male facial cues were presented, reaction time was significantly shorter in the congruent targets in the female but not male subjects. However, there were no significant differences in reaction time between the congruent and incongruent trials when the sexes of the facial stimuli were the same as those of the subjects. The current findings provide a first evidence of "opposite-sex effect" on gaze-guided social attention. These results further suggest that a biological value of faces is unconsciously estimated in a reflective and automatic manner to induce attention shift. Possible neural substrates for the present results are discussed.

Keywords: Face; Gaze; Sex; Attention; Social cognition

-
- 1) System Emotional Science, Graduate School of Medicine and Pharmaceutical Sciences, University of Toyama, Sugitani 2630, Toyama 930-0194, Japan
 - 2) CREST, JST, Tokyo, Japan
 - 3) Department of Neuropsychiatry, Graduate School of Medicine and Pharmaceutical Sciences, University of Toyama, Toyama, Japan

Correspondence should be addressed to;

*Dr. Hisao Nishijo

System Emotional Science, Graduate School of Medicine and Pharmaceutical Sciences, University of Toyama
Sugitani 2630, Toyama 930-0194

Japan

Tel: +81-76-434-7215

Fax: +81-76-434-5012

E-mail: nishijo@med.u-toyama.ac.jp

INTRODUCTION

Faces emit various social signals in our daily communication. We frequently use non-verbal information derived from faces for our communication such as emotional expression, gaze direction, identity, etc. It has been suggested that eyes have powerful social signals, and can be used to draw conclusions about other people's mental states (Baron-Cohen, 1997). Even 3-month old infants follow gazes of others (Hood et al., 1998), and this gaze following may lead to development of a full "Theory of Mind" (Premack and Woodruff, 1978). Baron-Cohen and his colleagues proposed that the brain contains several modules each specialized for different aspects of social existence (Baron-Cohen, 1997). In their model, an eye-direction detector identifies presence of eyes, their direction of gaze, and direct eye contact, and a second module for shared attention mechanisms identifies when the self and another are both attending to the same object or event. The latter process (shared attention process) allows for what Bruner terms joint attention (Bruner, 1983). Gaze-guided social attention, which underlies important processes for full expression of shared attention, can be assessed by the precueing method (Posner, 1978; Posner, 1980). In this method, a cue stimulus (precue) such as a facial image and a target such as a cross are presented successively with an intervening delay [stimulus onset asynchrony (SOA)]. Usually, the precue face gazes toward the right or left side where the targets appear after the SOA, which shifts subjects' attention to gaze direction of the facial stimulus (Driver et al., 1999; Langton and Bruce, 1999). The reaction time to detect the target stimulus is shorter on the side to which attention was directed by the seen gaze, which provides evidence of social attention (Driver et al., 1999; Langton and Bruce, 1999).

A previous study reported that various factors such as emotional expression and orientation of facial stimuli, which were presented as precue stimuli in the precueing paradigm, influenced gaze-

guided social attention (Hori et al., 2005). On the other hand, other previous psychological study reported that there was a sex difference in various cognitive processes (Maccoby and Jacklin, 1974). Generally, females perform better on tasks involving perceptual speed, comprehension and episodic memory, while males perform better on tasks involving visuospatial operations (Halpern, 1997). Regarding social skills, female scores are higher in emotion recognition (McClure, 2000; Thayer and Johnsen, 2000) and social sensitivity tests (Baron-Cohen et al., 1999). These studies suggest that females have higher social skills than males (see Baron-Cohen, 2005 for review). However, effects of sex differences on gaze detection ability and social attention mechanisms, which are involved in non-verbal communication skills, remains unknown. In the present study, we investigated an influence of sex of facial cues on gaze-guided social attention using the cueing method.

METHODS

Subjects

Fourteen subjects (male: $n=8$, female: $n=6$, average age 25.6 ± 1.18) participated in the present study. All subjects were right-handed with normal vision and naive to the purpose of the present experiment. All experimental procedures were carried out pertaining to the ethics code of our institution with adequate understanding and written consent of the subjects. Participants were tested individually.

Apparatus

A personal computer (IBM compatible) and a 15-inch color LCD monitor (LCD-A155GB, I-O Data Device Inc., Ishikawa, Japan) were used to present the stimuli using E-Prime software (Psychology Software Tools, Inc., PA, USA). The subjects were seated in a dark room, with their heads stabilized with a head holding device 60 cm apart from the display.

Materials

Facial stimuli as precue consisted of 8 upright images of 4 Japanese facial models (2 females and 2 males) in a frontal view with neutral facial expression. Each model gazed toward the right or left side of the display. These facial stimuli were selected from the ATR Database (Kamachi et al., 2001). Examples of the facial stimuli are shown

in Fig. 1. All of these photographs were subtended 16° in height, and 16° in width. The photographs were displayed using 8-bit RGB color levels on a black background. The target character of “+” (24 pitch) was displayed on the left or right side of the display (14° horizontally away from the center of the screen) on a black background.

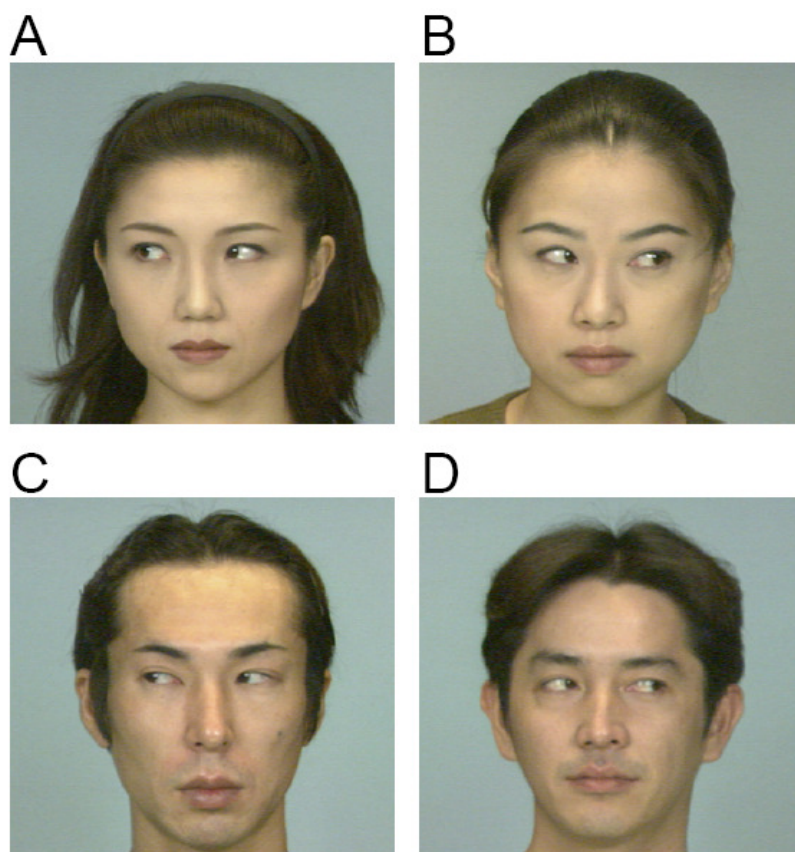


Fig. 1. Examples of facial stimuli used in a social attention task. Both female (A and B) and male (C and D) faces were used the experiment. These faces gazed toward the right or left side, which yielded 8 facial images.

Task procedures

Figure 2 shows a schematic depiction of a sequence of events within one trial. The general procedure for the present study was similar to those in our previous study (Hori et al., 2005) based on the precueing paradigm by Posner (Posner, 1978; Posner, 1980). Each trial was carried out in the same manner except for differences in the facial stimulus, SOA and congruity. Each experimental trial was initiated by a warning buzzer sound for

500 msec, which was immediately followed by a fixation cross appearing in the center of the display for 1500 msec. The subjects were required to fixate on this cross. Then, the fixation cross was replaced by a face, which also appeared in the center of the display followed by a target cross after a variable SOA. The targets were equally likely to appear on the left or right side of the display. The target cross and facial stimulus disappeared when the subject pressed a key.

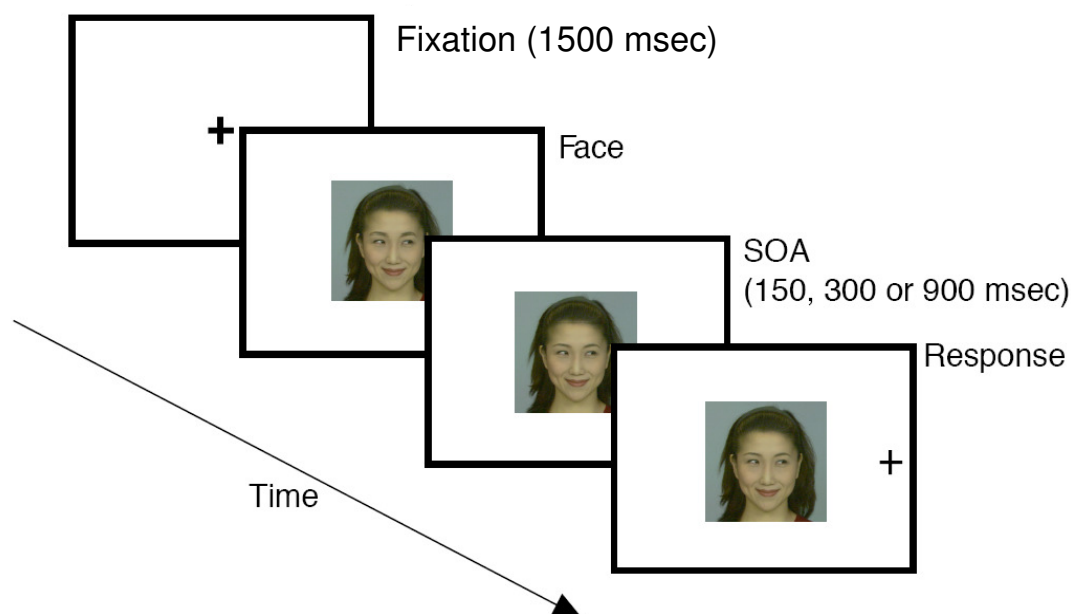


Fig. 2. Schematic illustration of an event sequence in a social attention task.

Each experimental trial was initiated by a warning buzzer sounding for 500 msec, followed by a cross in the center of a display to serve as a fixation point (1500 msec). Then, a female or male face gazing toward the right or left appeared in the center of the display, and was followed by a target cross that appeared at one (left or right) side of the display with variable SOAs.

The subjects were required to press a key that corresponded to the target location as quickly and accurately as possible with their preferred index fingers when they detected the targets. For example, if the target appeared on the left side, the subjects were required to press the "<" key; if the target appeared on the right side, they were required to press the ">" key. Pressing the keys automatically deleted the facial stimulus and the target from the display, and blacked out for 2000 msec until the next trial began. No information about the facial stimuli was given to the subjects. The subjects were not required to intentionally draw attention to gaze direction of the facial cues. Following parameters were recorded in each experimental trial; the name of facial cue (one of the 8 facial stimuli), the subject's response (right or left), the position of the target appearance (right or left) and reaction time (RT) for target detection. Before the experiments, the subjects were allowed to perform 4 practice trials to become acclimated to the experimental procedures. After the practice trials the subjects performed 96 trials over three blocks, which yielded 8 sets of the data for each experimental condition (a total of 12 within-subject conditions).

Data analysis

Incorrect responses and responses slower than 1000 msec were excluded from the analysis. All RT data were z-transformed for each subject to normalize the difference in RTs among the subjects. This normalization procedure is effective to analyze the data when the raw RTs differed largely among the subjects (Hori et al., 2005). The z-scores were averaged for each of the 12 conditions in each subject. Then, a grand mean of the z-scores in each of the 12 conditions was computed from the data of the all subjects, and presented as a mean±S.E.M. Statistical analysis was performed by a four-way ANOVA to reveal interaction among the 4 factors (SOA, congruity, facial model sex and subject sex). Subsidiary simple main effects were calculated to compare the mean z-scores between the 2 conditions of congruity (congruent vs. incongruent) in each SOA, and to compare the mean z-scores between the 2 conditions of congruity in each sex of the facial models. Subsequent multiple comparison analyses were performed by Ryan's method.

P-values less than 0.05 were defined as statistically significant.

RESULTS

A four-way analysis of variance (ANOVA) was designed to analyze reaction time (RT) for target detection using 3 within-subject and 1 between-subject factors in the present study. The first within-subject factor was SOA. The targets appeared after onset of the facial cues with variable intervals of SOA (150, 300 or 900 msec). The second within-subject factor was congruity between gaze direction and target position. In the congruent trials, the target appeared on the side that the cue face gazed toward. In the incongruent trials, the target appeared on the side opposite to that which the cue face gazed toward. The third within-subject factor was sex of the facial models (female or male). These within-subject factors were crossed to yield 12 experimental conditions in each subject. The between-subjects factor was sex of the subjects (female and male).

A four-way ANOVA for the averaged z-transformed data indicated a significant main

effect of congruity [$F(1,12)=22.426$, $P<0.01$]. Furthermore, significant interactions were detected between SOA and congruity [$F(2,24)=9.454$, $P<0.01$] and among sex of the facial models, sex of the subjects and congruity [$F(1,12)=5.458$, $P<0.05$].

Effects of SOA and congruity on RTs

Figure 3 shows a comparison of the mean z-scores between the 2 types of congruity in each SOA. The test of simple main effect of congruity in each SOA revealed significant effect at the SOA of 150 msec [$F(1,36)=30.351$, $P<0.01$] and 300 msec [$F(1,36)=10.980$, $P<0.01$], but no significant effect at the SOA of 900 msec [$F(1,36)=0.283$, $P>0.05$]. These results indicated that z-scores of RTs were significantly faster in the congruent trials than the incongruent trials at the SOA of 150 and 300 msec, and that there was no significant difference in the mean z-scores of RTs between the congruent and incongruent trials at the SOA of 900 msec.

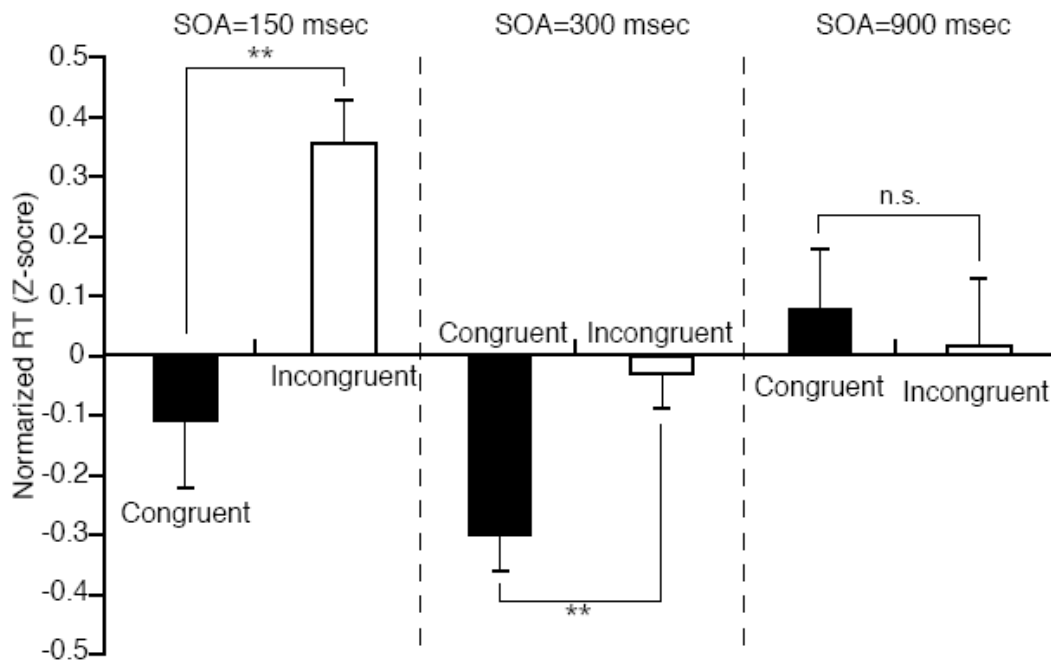


Fig. 3. Effects of SOA on z-transformed RTs.

Note that the mean z-scores were significantly lower in the congruent trials than incongruent trials at the SOA of 150 and 300 msec, but not at the SOA of 900 msec. Vertical axis, z-transformed reaction time (RT). **: Significant difference between the congruent and incongruent trials at the indicated SOA ($P < 0.01$).

Effects of sex and congruity on RTs

Figure 4 shows comparisons of the mean z-scores between the 2 congruities when the female and male facial models were presented to the female (A) and male (B) subjects. The test of simple main effect revealed a significant effect of congruity when the male faces were presented to the female subjects [$F(1,24) = 14.119$, $P < 0.01$], indicating

that the mean z-scores of RTs were significantly shorter in the congruent than incongruent trials when the male faces were presented to the female subjects (A). However, there was no significant simple main effect of congruity when the female faces were presented to the female subjects [$F(1,24) = 3.224$, $P > 0.05$].

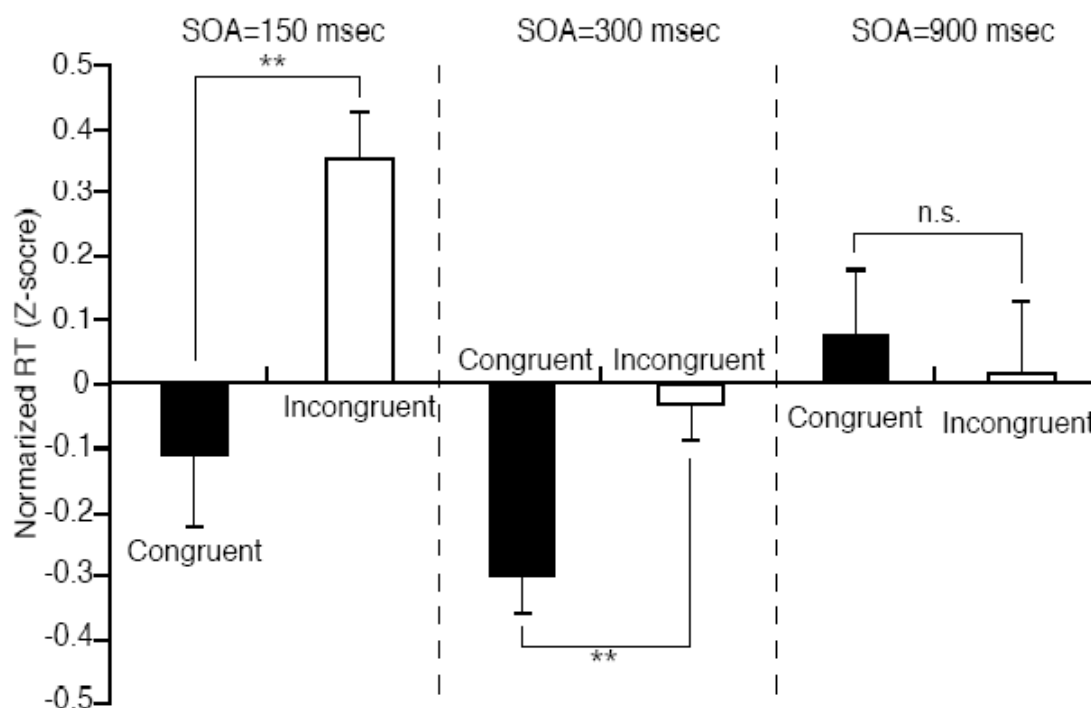


Fig. 4. Effects of sex of the facial cues on z-transformed RTs.

In the female subjects (A), the mean z-scores were significantly lower in the congruent trials than incongruent trials for the male faces (b), but not for the female faces (a). In the male subjects (B), the mean z-scores were significantly lower in the congruent trials than incongruent trials for the female faces (a), but not for the male faces (b). Vertical axis, z-transformed reaction time. **: Significant difference between the congruent and incongruent trials ($P < 0.01$).

In the male subjects, the test of simple main effect revealed a significant effect of congruity when the female faces were presented [$F(1,24) = 11.316$, $P < 0.01$], indicating that z-scores of RTs were significantly shorter in the congruent than incongruent trials when the female faces were presented to the male subjects (B). However, there was no significant simple main effect of congruity when the male facial models were presented to the male subjects [$F(1,24) = 0.569$, $P > 0.05$].

DISCUSSION

General characteristics of seen gaze-induced attention shift

In the present study at the short, but not long SOAs (SOA=150 and 300 msec), RTs to detect the targets were significantly faster in the

congruent trials in which gaze direction of the precue faces matched the locations of the targets than in the incongruent trials in which the precue faces gazed toward the side opposite to the target locations. These results provide evidence that seen gazes induce attention shift of the subjects, and are consistent with the previous extensive studies (Posner, 1978; Posner, 1980; Driver et al., 1999; Langton and Bruce, 1999; Hori et al., 2005; Bayliss et al., 2005; Friesen and Kingstone, 1998; Kingstone et al., 2000; Langton et al., 2000; Maner et al., 2003; Mathews et al., 2003).

Some studies reported inhibition of return (IOR) at long SOA (Friesen and Kingstone, 1998; Klein, 2000). IOR is reflected in the slower responding to the targets at the cued location, and is suggested to facilitate orienting to novel locations (Klein, 2000). In the present study, IOR was not observed in that a simple main effect of congruity

was not significant at the SOA of 900 msec. This absence of IOR is consistent with the previous precueing studies using gazes as precue (Driver et al., 1999; Bayliss et al., 2005), and IOR might be processes independent of gaze cueing effect (Friesen and Kingstone, 1998).

Characteristics of attention shift

Extensive studies have focused on the mechanisms of visual spatial attention using the precueing method (Posner, 1980; Jonides, 1981; Muller and Rabbitt, 1989; Posner and Cohen, 1984; Werner et al., 1990). The studies using non-facial visual precue suggest two types of mechanisms inducing spatial attention. One is an "exogenous" mechanism in which salient unpredictable peripheral cues induce spatial attention around the locations where the cues are presented. The above studies suggest that the processes for this attention shift are reflexive and automatic (i.e. under unconscious mechanisms) since 1) the SOA for the effective attention shift is relatively short (i.e., around 100-300 msec) and 2) this effect is stimulus-driven. The other is an "endogenous" mechanism, in which a visual precue, such as an arrow, induces an attention shift toward the direction of the arrow. This process is under voluntary or intentional control in which expectancy of an observer plays an important role.

Recently, the head and eye gaze direction of facial stimuli in the same precueing paradigm was reported to induce spatial attention shift through "exogenous" (reflective and automatic) processes since 1) the SOA for the effective attention shift was relatively short (i.e., around 100-300 msec) and 2) this effect occurred even though the gaze direction was uninformative to the location of the target (Driver et al., 1999; Langton and Bruce, 1999; Friesen and Kingstone, 1998; Kingstone et al., 2000; Mathews et al., 2003). These results suggest that facial stimuli automatically and unconsciously initiate social cognition processes of so-called "shared attention" (Bruner, 1983), "joint

attention" (Baron-Cohen, 1997), and "gaze following" (Butterworth and Jarrett, 1991) through this exogenous processes.

The above exogenous mechanisms also suggest that this attention shift is stimulus-driven. Therefore, both social and non-social components included in the precue faces could induce attention shift. Some evidence suggests that social meanings of the precue facial stimuli are important to induce attention shift. Previous studies indicated that facial expression of the precue faces modulated this gaze-induced attention shift (Hori et al., 2005; Mathews et al., 2003), and that the effects of facial expression on target detection disappeared when the precue facial stimuli were presented upside down (Hori et al., 2005). Furthermore, a recent clinical study using human patients with brain damages suggests that different neural mechanisms are involved in attention shift induced by arrows and gazed faces (Akiyama et al., 2006). These results strongly suggest that attention shift of the subjects observed in the present study was attributed to social meanings but not by non-social components of the precue faces.

Taken together, all available evidence suggests that attention shift observed in the present study was mediated through exogenous mechanisms in a reflective and automatic manner, and suggests that modulation of attention by the faces of opposite sex (see below) is also mediated through these mechanisms.

Opposite-sex effects on gaze-guided attention shift

Maner et al. (2003) reported that both male and female subjects fixate on the faces of opposite sex longer than those of the same sex. This finding suggests that subjects pay more attention to faces of opposite sex than to those of the same sex. In the present study, significant main effects of congruity were observed in the male faces for the female subjects and in the female faces for the male subjects. The present results provide first evidence

of "opposite-sex effect" on gaze-guided attention shift. An attractive opposite sex faces may emit a signal as a potential for sexual partner (Senior, 2003), and might be biologically or emotionally positive and rewarding. This emotionally positive and/or rewarding valence of the opposite sex faces may facilitate reflexive gaze-guided attention shift. Consistently, faces with happy emotional expression were more effective than those with anger emotional expression to facilitate reflexive attention shift (Hori et al., 2005). Furthermore, a previous study suggested that facial attractiveness was evaluated in a reflective and automatic manner (Olson and Marshuetz, 2005). These results suggest that biological value of faces is unconsciously estimated in a reflective and automatic manner to induce attention shift.

Previous studies indicated that seen female faces are more superior to male faces in attractiveness (Maner et al., 2003; Kranz and Ishai, 2006), emotion discrimination (Thayer and Johnsen, 2000), recognition and gender classification (Becker et al., 2005; O'Toole et al., 1988). In the present study, no obvious advantage of the female faces was observed, suggesting that this is true for social attention mechanisms. Although the main effect of congruity was statistically insignificant when the female faces were presented to the female subjects, this effect was marginally significant ($P=0.085$). These results suggest that the female faces might be more effective to facilitate gaze-guided social attention. Further studies are required to investigate effects of sex difference of facial models on gaze-induced social attention.

Neural substrates for gazing effects

Recently, Akiyama et al. (2006) reported that a patient with lesions in the right superior temporal gyrus showed severe impairment of target detection that cued by gazing faces but not by non-biological symbols such as an arrow (Akiyama et al., 2006). A neurophysiological study indicated that neurons in the macaque superior temporal sulcus

(STS) were sensitive to gaze direction (Perrett et al., 1998). Extensive non-invasive studies reported that the human STS was activated during viewing or detecting gaze direction of other individuals (Friesen and Kingstone, 1998; Hoffman and Haxby, 2000; Hooker et al., 2003; Kingstone et al., 2004; Pelphrey et al., 2003; Puce et al., 1998; Puce et al., 2000; Taylor et al., 2001; Wicker et al., 1998). These studies indicate that the STS is a key structure in the brain to detect gaze direction of other individuals.

In addition to the STS, the amygdala (Adams et al., 2003; Kawashima et al., 1999), intraparietal sulcus and fusiform face area (Pelphrey et al., 2003) are also reported to play an important role in gaze detection. The amygdala is a core system for biological evaluation of various environmental stimuli such as food or foot shock (Nishijo et al., 1998a,b; Phillips and LeDoux, 1992). It has been reported that the human amygdala and adjacent anterior temporal regions of male subjects were activated during exposure to female faces (Fischer et al., 2004). All of these studies suggest that the temporal regions including the STS and amygdala are essential for opposite-sex effect on gaze-guided attention shift.

Kranz and Ishai (2006) analyzed brain activity of heterosexual and homosexual subjects when they saw sexually preferred and non-preferred faces to them. Regardless of their biological sexes, sexually preferred faces activated the mediodorsal thalamus and medial orbitofrontal cortex in both the heterosexual and homosexual subjects. The medial orbitofrontal cortex is involved in representing reward value of various environmental stimuli (Rolls, 2004) including facial attractiveness (O'Doherty et al., 2003). Taken together, these results suggest that a neural network including the medial orbitofrontal cortex, amygdala and STS are important to evaluate social stimuli such as sexual attractiveness, gaze direction, etc. These neural circuits might underlie the shared attention mechanisms and other modules for mind reading mechanisms that proposed by Baron-Cohen (Baron-Cohen, 1997).

Conclusions

We found "opposite-sex effect" on gaze-guided attention shift in the present study. These results further suggest that a biological value of faces is unconsciously estimated in a reflective and automatic manner to induce attention shift. Along with the other previous studies, it is suggested that a neural network including the medial orbitofrontal cortex, amygdala and STS are important to evaluate social stimuli such as sexual attractiveness, gaze direction, etc. to affect gaze-directed social attention.

Acknowledgments:

This work was supported partly by the JSPS Asian Core Program.

REFERENCES

- Adams, R. B., Gordon, H. L., Baird, A. A., Ambady, N., Kleck, R. E., 2003. Effects of gaze on amygdala sensitivity to anger and fear faces. *Science* 300, 1536.
- Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Umeda, S., Kashima, H., 2006. Gaze but not arrows: A dissociative impairment after right superior temporal gyrus damage. *Neuropsychologia* 44, 1804-1810.
- Baron-Cohen, S., 1997. *Mindblindness: An essay on autism and theory of mind*. MIT Press, Cambridge, USA.
- Baron-Cohen, S., O'Riordan, M., Stone, V., Jones, R., Plaisted, K., 1999. Recognition of faux pas by normally developing children and children with Asperger syndrome or high-functioning autism. *J. Autism Dev. Disord.* 29, 407-418.
- Baron-Cohen, S., Knickmeyer, R. C., Belmonte, M. K., 2005. Sex differences in the brain: Implications for explaining autism. *Science* 310, 819-823.
- Bayliss, A. P., di Pellegrino, G., Tipper, S. P., 2005. Sex differences in eye gaze and symbolic cueing of attention. *Q. J. Exp. Psychol.* 58, 631-650.
- Becker, D. V., Kenrick, D. T., Guerin, S., Maner, J. K., 2005. Concentrating on beauty: Sexual selection and sociospatial memory. *Pers. Soc. Psychol. B.* 31, 1643-1652.
- Bruner, J., 1983. *Child's talk: Learning to use language*. Oxford University Press, Oxford, UK.
- Butterworth, G., Jarrett, N., 1991. What minds have in common is space: Spatial mechanisms serving joint visual attention in infancy. *Brit. J. Dev. Psychol.* 9, 55-72.
- Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., Baron-Cohen, S., 1999. Gaze perception triggers reflexive visuospatial orienting. *Vis. Cogn.* 6, 509-540.
- Fischer, H., Sandblom, J., Herlitz, A., Fransson, P., Wright, C. I., Backman, L., 2004. Sex-differential brain activation during exposure to female and male faces. *Neuroreport* 15, 235-238.
- Friesen, C. K., Kingstone, A., 1998. The eyes have it!: Reflexive orienting is triggered by nonpredictive gaze. *Psychon. B. Rev.* 5, 490-495.
- Halpern, D. F., 1997. Sex differences in intelligence: Implications for education. *Am. Psychol.* 52, 1091-1102.
- Hoffman, E. A., Haxby, J. V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nat. Neurosci.* 3, 80-84.
- Hood, B. M., Willen, J. D., Driver, J., 1998. Adult's eyes trigger shifts of visual attention in human infants. *Psychol. Sci.* 9, 53-56.
- Hooker, C. I., Paller, K. A., Gitelman, D. R., Parrish, T. B., Mesulam, M. M., Reber, P. J., 2003. Brain networks for analyzing eye gaze. *Cognitive Brain Res.* 17, 406-418.
- Hori, E., Tazumi, T., Kobayashi, T., Umeno, K., Kamachi, M., Ono, T., Nishijo, H., 2005. Effects of facial expression on shared attention mechanisms. *Physiol. Behav.* 84, 397-405.
- Jonides, J., 1981. Voluntary versus automatic

- control over the mind's eye's movement. In *Attention and performance. IX.* Long, J. B., Baddely, A. D., Eds. Lawrence Erlbaum Associates, Hillsdale, NJ, pp187-203.
- Kamachi, M., Bruce, V., Mukaida, S., Gyoba, J., Yoshikawa, S., Akamatsu, S., 2001. Dynamic properties influence the perception of facial expressions. *Perception* 30, 875-887.
- Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Ito, K., Fukuda, H., Kojima, S., Nakamura, K., 1999. The human amygdala plays an important role in gaze monitoring. A PET study. *Brain* 122, 779-783.
- Kingstone, A., Friesen, C. K., Gazzaniga, M. S., 2000. Reflexive joint attention depends on lateralized cortical connections. *Psychol. Sci.* 11, 159-166.
- Kingstone, A., Tipper, C., Ristic, J., Ngan, E., 2004. The eyes have it! An fMRI investigation. *Brain Cognition* 55, 269-271.
- Klein, R. M., 2000. Inhibition of return. *Trends Cogn. Sci.* 4, 138-147.
- Kranz, F., Ishai, A., 2006. Face perception is modulated by sexual preference. *Curr. Biol.* 16, 63-68.
- Langton, S. R. H., Bruce, V., 1999. Reflexive visual orienting in response to the social attention of others. *Vis. Cogn.* 6, 541-567.
- Langton, S. R. H., Watt, R. J., Bruce, V., 2000. Do the eyes have it? Cues to the direction of social attention. *Trends Cogn. Sci.* 4, 50-59.
- Maccoby, E. E., Jacklin, C. N., 1974. *The psychology of sex differences.* Stanford University Press, CA, USA.
- Maner, J. K., Kenrick, D. T., Becker, D. V., Delton, A. W., Hofer, B., Wilbur, C. J., Neuberg, S. L., 2003. Sexually selective cognition: Beauty captures the mind of the beholder. *J. Pers. Soc. Psychol.* 85, 1107-1120.
- Mathews, A., Fox, E., Yiend, J., Calder, A., 2003. The face of fear: Effects of eye gaze and emotion on visual attention. *Vis. Cogn.* 10, 823-835.
- McClure, E. B., 2000. A meta-analytic review of sex differences in facial expression processing and their development in infants, children, and adolescents. *Psychol. Bull.* 126, 424-453.
- Muller, H. J., Rabbitt, P. M. A., 1989. Reflexive and voluntary orienting of visual attention: Time course and resistance to interruption. *J. Exp. Psychol.* 15, 315-330.
- Nishijo, H., Ono, T., Nishino, H., 1988a. Single neuron responses in amygdala of alert monkey during complex sensory stimulation with affective significance. *J. Neurosci.* 8, 3570-3583.
- Nishijo, H., Ono, T., Nishino, H., 1988b. Topographic distribution of modality-specific amygdalar neurons in alert monkey. *J. Neurosci.* 8, 3556-3569.
- O'Doherty, J., Winston, J., Critchley, H. D., Perrett, D., Burt, D. M., Dolan, R. J., 2003. Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia* 41, 147-155.
- Olson, I. R., Marshuetz, C., 2005. Facial attractiveness is appraised in a glance. *Emotion* 5, 498-502.
- O'Toole, A. J., Deffenbacher, K. A., Valentin, D., McKee, K., Huff, D., Abdi, H., 1988. The perception of face gender: The role of stimulus structure in recognition and classification. *Mem. Cognition* 26, 146-160.
- Pelphrey, K. A., Singerman, J. D., Allison, T., McCarthy, G., 2003. Brain activation evoked by perception of gaze shifts: The influence of context. *Neuropsychologia* 41, 156-170.
- Perrett, D. I., Oram, M. W., Ashbridge, E., 1998. Evidence accumulation in cell populations responsive to faces: An account of generalization of recognition without mental transformations. *Cognition* 67, 111-145.
- Phillips, R. G., LeDoux, J. E., 1992. Differential contribution of amygdala and hippocampus to cues and contextual fear conditioning. *Behav. Neurosci.* 106, 274-285.
- Posner, M. I., 1978. *Chronometric explorations of mind.* Lawrence Erlbaum Associates, Hillsdale, NJ.
- Posner, M. I., 1980. Orienting of attention. *Q. J.*

- Exp. Psychol. 32, 3-25.
- Posner, M. I., Cohen, Y., 1984. Components of visual orienting. In Attention and performance. X. Bouma, H., Bouwhuis, D. G., Eds, Lawrence Erlbaum Associates, Hillsdale, NJ, pp531-556.
- Premac, D., Woodruff, G., 1978. Dose the chimpanzee have a theory of mind? Behav. Brain Sci. 1, 515-526.
- Puce, A., Allison, T., Bentin, S., Gore, J. C., McCarthy, G., 1998. Temporalcortex activation in humans viewing eye and mouth movements. J. Neurosci. 18, 2188-2199.
- Puce, A., Smith, A., Allison, T., 2000. ERPs evoked by viewing facial movements. Cogn. Neuropsychol. 17, 221-239.
- Rolls, E. T., 2004. The functions of the orbitofrontal cortex. Brain Cognition 55, 11-29.
- Senior, C., 2003. Beauty in the brain of the beholder. Neuron 38, 525-528.
- Taylor, M. J., Itier, R. J., Allison, T., Edmonds, G. E., 2001. Direction of gaze effects on early face processing: Eyes-only versus full faces. Cognitive Brain Res. 10, 333-340.
- Thayer, J. F., Johnsen, B. H., 2000. Sex differences in judgement of facial affect: A multivariate analysis of recognition errors. Scand. J. Psychol. 41, 243-246.
- Werner, C. B., Juola, J. F., Koshino, H., 1990. Voluntary allocation versus automatic capture of visual attention. Percept. Psychophys. 48, 234-251.
- Wicker, B., Michel, F., Henaff, M. A., Decety, J., 1998. Brain regions involved in the perception of gaze: A PET study. Neuroimage 8, 221-227.