Effects of direct and averted gaze on the subsequent saccadic response

Hiroshi Ueda • Kohske Takahashi • Katsumi Watanabe

Published online: 14 March 2014 © Psychonomic Society, Inc. 2014

Abstract The saccadic latency to visual targets is susceptible to the properties of the currently fixated objects. For example, the disappearance of a fixation stimulus prior to presentation of a peripheral target shortens saccadic latencies (the gap effect). In the present study, we investigated the influences of a social signal from a facial fixation stimulus (i.e., gaze direction) on subsequent saccadic responses in the gap paradigm. In Experiment 1, a cartoon face with a direct or averted gaze was used as a fixation stimulus. The pupils of the face were unchanged (overlap), disappeared (gap), or were translated vertically to make or break eye contact (gaze shift). Participants were required to make a saccade toward a target to the left or the right of the fixation stimulus as quickly as possible. The results showed that the gaze direction influenced saccadic latencies only in the gaze shift condition, but not in the gap or overlap condition; the direct-to-averted gaze shift (i.e., breaking eye contact) yielded shorter saccadic latencies than did the averted-to-direct gaze shift (i.e., making eve contact). Further experiments revealed that this effect was eye contact specific (Exp. 2) and that the appearance of an eye gaze immediately before the saccade initiation also influenced the saccadic latency, depending on the gaze direction (Exp. 3). These results suggest that the latency of targetelicited saccades can be modulated not only by physical changes of the fixation stimulus, as has been seen in the conventional gap effect, but also by a social signal from the attended fixation stimulus.

Keywords Eye contact \cdot Gap effect \cdot Gaze perception \cdot Saccade

H. Ueda (🖂) • K. Takahashi • K. Watanabe

Research Center for Advanced Science and Technology, University of Tokyo, 4-6-1 Komaba, Meguro-ku, Tokyo 153-8904, Japan e-mail: uedahi64@fennel.rcast.u-tokyo.ac.jp

High visual acuity in the human eye is restricted to a small region in the central retina (the fovea); hence, people need to continually make saccades in order to grasp a visual scene. Thus, one critical factor to efficiently scan the visual field is how quickly we can move fixations from one location to another. The efficiency of saccadic travel has been examined by a target-elicited saccade paradigm, in which participants are asked to fixate one location initially and then to make a saccade toward a target that appears at another location.

Studies with the target-elicited saccade paradigm have suggested that various factors influence the saccadic latency. For instance, a bright target stimulus leads to a faster saccadic reaction than does a dim target (Boch, Fischer, & Ramsperger, 1984; Kalesnykas & Hallett, 1994; Reuter-Lorenz, Hughes, & Fendrich, 1991), suggesting that high-intensity stimuli reach one's perceptual threshold faster (Bell, Meredith, Van Opstal, & Munoz, 2006). Target locations also matter: The distance (i.e., retinal eccentricity) and relative direction of a target from the initially fixated location affect saccadic latency. The saccadic latency is shorter when a target eccentricity is between approximately 1° and 10°, and it increases with smaller or larger eccentricities (Kalesnykas & Hallett, 1994). The saccadic latency also tends to be shorter when a target is presented in a horizontal direction than when it is presented in a vertical direction (Vernet, Yang, Gruselle, Trams, & Kapoula, 2009).

The influence of the target properties on the saccadic latency seems intuitive. However, the properties of the initially fixated stimuli also influence the subsequent saccadic latency (Reuter-Lorenz et al., 1991; Vernet et al., 2009). In particular, if a fixation stimulus disappears shortly (approximately 200 ms) before the presentation of a peripheral target (gap condition), the saccadic latency to the target is shorter than if the fixation stimulus had remained present (overlap condition). This phenomenon was first reported by Saslow (1967) and is termed the *gap effect* (e.g., Dorris & Munoz,

1995; Fischer & Ramsperger, 1984; Kalesnykas & Hallett, 1987; Kingstone & Klein, 1993; Reuter-Lorenz et al., 1991). The gap effect is a robust phenomenon that occurs across variations in target intensity (Reuter-Lorenz et al., 1991), target location (Vernet et al., 2009), and expectancy of the target location (Kingstone & Klein, 1993; Walker, Kentridge, & Findlay, 1995).

The gap effect demonstrates that the saccadic latency is influenced by several factors of a previously fixated location. First, physical changes of a fixation point (e.g., onset/offset or changes in size, luminance, color, etc.) preceding a target presentation can serve as a temporal cue that induces saccade preparation, which results in shorter saccadic latencies (the general warning effect; Jin & Reeves, 2009; Kingstone & Klein, 1993; Pratt, Bekkering, & Leung, 2000; Reuter-Lorenz et al., 1991; L. E. Ross & Ross, 1980; S. M. Ross & Ross, 1981). Among those physical changes of fixation stimuli, the "disappearance" induces the strongest response facilitation. This effect is specifically termed the fixation offset effect (Fendrich, Hughes, & Reuter-Lorenz, 1991; Kingstone & Klein, 1993; Munoz & Wurtz, 1992; Reuter-Lorenz et al., 1991), and its neural substrate has been found in the superior colliculus of nonhuman primates (e.g., Dorris & Munoz, 1995; Munoz & Wurtz, 1992). The facilitation of saccadic latencies due to the physical changes may reflect the bottomup processes of making saccadic eye movements; however, top-down factors can also affect the subsequent saccadic responses. Pratt, Lajonchere, and Abrams (2006) demonstrated that covert attention to a fixation can modulate the response facilitation of the gap effect. They showed that the disappearance of an attended portion of a fixation stimulus causes larger response facilitation than disappearance of an unattended portion. Moreover, in a recent study, we demonstrated that expectation of the reappearance of the fixation stimulus that was hidden by a moving occluder interferes with the response facilitation in the gap effect (Ueda, Takahashi, & Watanabe, 2013). Thus, the subjective impression of a fixation stimulus can also modulate the saccadic latency, in addition to physical changes of the fixation stimulus.

Given the top-down modulations of the influences of fixation properties on subsequent saccades, in the present study we aimed to further elucidate whether cognitive interpretation of a visual event, particularly that of gaze shift, influences response facilitation in the gap-overlap paradigm. As a social signal, direct gaze (eye contact) from others carries a wealth of social information. Although the physical difference in visual images between direct gaze and averted gaze is subtle, eye contacts from others have a special social implication (for reviews, see Emery, 2000; Senju & Johnson, 2009). Several studies have reported that people were highly sensitive to direct gaze from others. For instance, in the visual search paradigm, detecting a direct-gaze target among averted-gaze distractors is easier than detecting an averted-gaze target among direct-gaze distractors (Conty, Tijus, Hugueville, Coelho, & George, 2006; Doi & Ueda, 2007; Palanica & Itier, 2011; Senju, Hasegawa, & Tojo, 2005; von Grünau & Anston, 1995). In addition, Senju and Hasegawa (2005) demonstrated that direct gaze could capture spatial attention and interfere with attentional disengagement (i.e., breaking eye contact).

In the present study, we investigated how a visual stimulus with a social signal (i.e., eye contact) modulates subsequent response facilitation in the gap effect. More specifically, we used the eyes (i.e., pupils) of a cartoon face that indicated either a direct gaze or an averted gaze as the fixation stimulus. The eyes disappeared 200 ms prior to the target onset in the gap condition or remained present in the overlap condition. In addition to those temporal-gap and overlap conditions, we also examined a change in the state of eye contact (i.e., breaking vs. making eye contact) of a cartoon fixation stimulus 200 ms prior to the target onset. Therefore, even though the physical changes between those two stimuli were nearly identical (i.e., vertical shift of the pupils), they would have different meanings to observers in terms of a social signal. In Experiment 2, we investigated the effects of geometric properties of the fixation stimuli by removing facial features. In addition to a shift of gaze directions, in Experiment 3 we further investigated the effect of the abrupt presentation of direct and averted gazes in the gap-overlap paradigm.

Experiment 1

Method

Participants A group of 20 paid volunteers (14 women, six men; age range 19–33 years, mean age 22.6 years) participated in the experiment. All had normal or corrected-to-normal vision, and all gave written informed consent before the experiment.

Experimental setting and apparatus The experiment was performed in a dark room. The participants sat with their heads stabilized on a chinrest mounted at a viewing distance of 57 cm. Visual stimuli were generated using the MATLAB Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and Eyelink Toolbox extensions and were displayed on a 21-in. CRT monitor with a 100-Hz refresh rate. Eye movements were recorded by the EyeLink 1000 eyetracker system with MATLAB Eyelink Toolbox extensions (Cornelissen, Peters, & Palmer, 2002).

Stimuli The visual stimuli are schematically depicted in Fig. 1. A cartoon face, which consisted of a round gray face surface (2.5° in a diameter, 10.3 cd/m^2), a lined nose and mouth (1.2 cd/m^2), and scleras (the whites of the eyes: 0.7°



Fig. 1 Stimuli and trial sequences in Experiment 1. A trial started with the presentation of a cartoon face with direct or averted gaze that served as the fixation stimulus. Then, the pupils of the face disappeared (gap), shifted vertically, or remained as they were (overlap). After a 200-ms delay period, a target dot appeared to the left or right of the fixation face for 1,000 ms. The participants were asked to fixate on the eyes of the cartoon face and then to make a saccade toward the target as quickly as possible

in a diameter, 64.2 cd/m^2) and pupils (0.2° in a diameter, 1.2 cd/m^2), was presented at the center of the screen. The pupils of the eyes were placed either at the center of the scleras, for direct gaze, or 0.2° above/below the center, for averted gaze. A white target dot (2.5° , 37.9 cd/m^2) was presented 8.0° to the left or right of the center of the face. All of the stimuli were presented against a black background (0.2 cd/m^2).

Procedure Each trial began with presentation of the cartoon face, which had either a direct or an averted gaze, for 1,000–2,000 ms (Fig. 1). The participants were required to fixate on the eyes of the face rather than on the face as a whole. No instruction was given as to which eye to fixate on (i.e., left or right). Then, the pupils were removed from the stimuli (gap), were kept unchanged (overlap), or were displaced vertically. After a 200-ms delay period, a peripheral target appeared to the left or right of the fixation stimulus. Participants were asked to make a saccade toward the target as quickly as possible. Trials were interleaved with 1,000-ms intervals, which were announced by an acoustic tone.

The experiment had a 2×3 within-participants design of the initial gaze direction (direct or averted) and the fixation condition (gap, shift, or overlap). We were particularly interested in the shift conditions, in which gaze was initially direct and then changed to averted, or was initially averted and then changed to direct. Although the stimulus configurations were quite similar, the former case is suggestive of breaking eye contact (i.e., disappearance of the direct gaze), whereas the latter case is suggestive of making eye contact (i.e., appearance of the direct gaze).

The experiment consisted of 192 trials, in which the six stimulus conditions were intermixed and presented in random order. Before the experiment, the eyetracker was calibrated for each participant using nine reference points. Drift correction of the eyetracker was also conducted every 48 trials. Participants were allowed to take a short break prior to the drift correction if they needed.

Data acquisition Eye movements were recorded at a sampling rate of 500 Hz. The saccadic latency was defined as the time elapsed from the target onset to a saccade onset, where the saccade onset was defined as the time at which the eye velocity exceeded a threshold of 30° /s.

Trials with a saccadic latency less than 80 ms or greater than 700 ms were excluded from further analyses, because anticipatory responses and a lack of participant alertness, respectively, were assumed (Reuter-Lorenz et al., 1991). All trials with incorrect responses were also excluded from analysis. Trials were considered incorrect if the initial gaze direction subsequent to target onset was in the wrong direction, even if the direction was subsequently corrected. These criteria were also applied to the following experiments, and overall, 2 % of trials were removed from the analysis.

Results and discussion

The mean saccadic latencies are shown in Table 1 and Fig. 2. A 2 (initial gaze directions) \times 3 (fixation conditions) repeated measures analysis of variance (ANOVA) revealed significant main effects of the initial gaze direction [F(1, 19) = 9.51, p <.01, $\eta_p^2 = .33$] and fixation condition [F(2, 38) = 42.28, p < .001, $\eta_p^2 = .69$], as well as a significant interaction [F(2, 38) = 6.36, p < .01, $\eta_p^2 = .25$]. Multiple comparisons of the fixation condition showed that the saccadic latencies were longer in the order gap, shift, and overlap (Bonferroni-corrected p < .01, r > .70 for all pairs). The significant interaction indicated that an effect of the initial gaze direction was found only in the shift condition [F(1, 19) = 14.04, p < .01, $\eta_p^2 = .43$] but in neither the gap [F(1, 19) = 1.54, p = .23, $\eta_p^2 < .08$] nor the overlap $[F(1, 19) = 1.27, p = .27, \eta_p^2 < .06]$ condition. Moreover, multiple comparisons of the fixation condition in each initial gaze direction showed significant differences between all pairs (Bonferroni-corrected p < .01, r > .50).

Experiment 1 ($N = 20$)	Fixation Condition		
Initial Gaze Direction	Gap	Shift	Overlap
Direct	192	202	227
Averted	195	215	229
Experiment 2 ($N = 20$)	Fixation Condition		
Initial Fixation Position	Gap	Shift	Overlap
Center	198	228	248
Periphery	201	234	251
Experiment 3 ($N = 20$)	Fixation Condition		
Final Gaze Direction	Appearance	Shift	Overlap
Direct	236	219	251
Averted	225	211	256

Table 1 Mean saccadic latencies (ms) in Experiments 1, 2, and 3

Of particular interest in Experiment 1 was how the direction of the gaze (i.e., direct vs. averted) affected saccadic latencies in each fixation condition (i.e., gap, shift, overlap). The results demonstrated that gaze direction affected only the gaze shift condition, but not the gap or overlap conditions. These results indicate that the shift of gaze direction in the fixation stimulus, breaking or making eye contact, shortly before a target onset had an effect to alter the observers' subsequent saccade, and the gaze direction by itself did not convey a strong enough signal to alter the gap effect. To further discuss these results, in the next experiment we examined how the physical properties of the fixation stimulus, rather than the social signal of eye contact, contributed to the result pattern of Experiment 1.

Experiment 2



The results of Experiment 1 implied that (dis)appearance of eye contact signal from the fixation stimulus could modulate the subsequent saccadic response. However, although the distances of pupil displacement were the same between the

Fig. 2 Mean saccadic latencies of each condition in Experiment 1. The error bars represent the within-participants standard errors of the means

direct-to-averted and averted-to-direct stimuli in the shift condition of Experiment 1, the positions of the pupil relative to the sclera were not; the pupils were shifted from the center of the scleras to their periphery in the direct-to-averted shift, whereas they were shifted from the periphery to the center in the averted-to-direct shift. Therefore, it is possible that these differences in the stimulus properties, rather than the social signal of eye contact, yielded the difference in the response facilitation. In Experiment 2, therefore, we modified the fixation stimulus such that it would not be interpreted as a face. In particular, we used only a single pupil and the sclera of the eye, while removing all other parts of the face (Fig. 3).

Method

A group of 20 paid participants who had not taken part in Experiment 1 were recruited (five women, 15 men; age range 19–29 years, mean age 21.6 years). All had normal or corrected-to-normal vision and gave written informed consent prior to the experiment. The same experimental stimuli and procedures were used as in Experiment 1, except that a single dot within a white disk (i.e., the pupil and the sclera of a single eye in Exp. 1) was used as the fixation stimulus and was presented at the center of the screen. All the participants were



Fig. 3 Stimuli and trial sequences of each condition in Experiment 2. The pupil (black dot) and sclera (white disk) of a single eye in Experiment 1 were used as the experimental stimuli, and the participants were asked to fixate on the black dot within the white disk. Otherwise, all of the sequences were the same as in Experiment 1

asked if they perceived the fixation stimulus as an eye after the experiment.

Results and discussion

None of the participants reported perceiving the fixation stimulus as an eye. The results of Experiment 2 are shown in Table 1 and Fig. 4. A 2 (initial fixation positions) \times 3 (fixation conditions) repeated measures ANOVA showed a significant main effect of the fixation condition [F(2, 38) = 13.93], p < .001, $\eta_p^2 = .42$]. However, unlike the facial fixation stimulus in Experiment 1, neither the main effect of the initial fixation position nor the interaction was significant [F(1, 19) =2.20, p = .15, $\eta_p^2 = .10$, and F(1, 19) = 0.67, p = .52, $\eta_p^2 = .03$, respectively]. Multiple comparisons of the fixation condition (Bonferroni corrected) showed that the saccadic latency of the gap condition was significantly shorter than that of the shift and overlap conditions (p < .05, r = .52, and p < .01, r = .89, respectively), and the saccadic latency of the shift condition tended to be shorter than that of the overlap condition (p = .07, r = .40).

The results showed that the position of the dot in the disk caused no effect in any of the fixation conditions. These results imply that modulation of the gap effect by the gaze shifts in Experiment 1 was not due to a geometric property of the fixation stimulus, but was likely to be due to the interpretation of a social signal from the gaze shift.

Experiment 3

Experiments 1 and 2 showed that shift of the gaze direction of a fixation stimulus influenced the subsequent saccadic latency, depending on its probable interpretation as a social signal (i.e., the appearance or disappearance of eye contact). In Experiment 3, we tested whether the abrupt appearance of a direct or



Fig. 4 Mean saccadic latencies of each condition in Experiment 2. The error bars represent the within-participants standard errors of the means

averted gaze shortly before the target onset, rather than the shift of the gaze direction, was sufficient to influence the subsequent saccadic latency. In Experiment 3, we tested a condition in which the eyes without a pupil were initially presented, and then the direct or averted gaze abruptly appeared before the target onset.

Method

A group of 20 paid volunteers participated, among whom five had participated in Experiment 1 and another ten had participated in Experiment 2 (five women, 15 men; age range 19– 24 years, mean age 21.0 years). All had normal or correctedto-normal vision and gave written informed consent prior to the experiment. The experimental stimuli are depicted in Fig. 5. We used the same facial fixation stimulus as in Experiment 1, except that the pupils were not displayed during the initial fixation period. Participants were asked to fixate on the eyes of the face rather than on the face as a whole. The pupils of the eyes appeared either in the center (direct gaze) or in the upper/lower periphery (averted gaze) of the sclera 200 ms before the target presentation. The rest of the stimuli and procedures were identical to those of Experiments 1 and 2.



Fig. 5 Stimuli and trial sequences of Experiment 3. The gap condition in Experiment 1 was replaced with a sudden-gaze-appearance condition, in which the facial stimulus of Experiment 1, but with no pupils, was used as the initial fixation stimulus, and then the pupils were presented in the center (direct gaze) or in the upper/lower periphery (averted gaze) of the scleras 200 ms before the target onset. The shift and overlap conditions were the same as in Experiment 1

Results and discussion

The mean saccadic latencies are shown in Table 1 and Fig. 6. A 2 (final gaze directions) \times 3 (fixation conditions) repeated measures ANOVA showed significant main effects of the final gaze direction $[F(1, 19) = 7.63, p < .05, \eta_p^2 < .29]$ and fixation condition $[F(2, 38) = 13.68, p < .001, \eta_p^2 = .42]$, as well as a significant interaction $[F(2, 38) = 5.43, p < .01, \eta_p^2 < .22].$ Multiple comparisons of the fixation condition showed that the saccadic latencies were longer in the order shift, appearance, and overlap condition (Bonferroni-corrected p < .05, r >.49 for all pairs). Further analyses revealed that the final gaze direction influenced the saccadic latency in the shift condition $[F(1, 19) = 4.73, p < .05, \eta_p^2 = .20]$, replicating the results of Experiment 1. Furthermore, we also found a statistically significant effect of gaze direction in the appearance condition $[F(1, 19) = 11.98, p < .01, \eta_p^2 = .39]$. In the overlap condition, the influence of gaze direction was absent [F(1, 19) = 2.24, p =.15, $\eta_p^2 < .11$]. Moreover, multiple comparisons of the fixation condition for each final gaze direction showed a significant difference between all pairs (Bonferroni-corrected p < .05, r >.48), except between the appearance and shift conditions when the final gaze direction was averted (p < .14, r = .33).

Thus, the results of Experiment 3 showed that the influence of the abrupt appearance of the eyes on the subsequent saccadic latency was also different in magnitude depending on the gaze directions. The consistent results between the appearance and shift conditions (i.e., the saccadic latencies were longer when the final fixation was a directed gaze) indicate that the gaze direction immediately before saccades is crucial; however, since the influence of the gaze direction was absent in the overlap conditions of Experiments 1 and 3, we conjecture that the effect of the social signal from the gaze direction would be short-lived. In addition to the effects of the gaze direction, the results of Experiment 3 also showed the different effects of the fixation condition. The shorter latencies in the appearance and shift conditions than in the overlap



Fig. 6 Mean saccadic latencies of each condition in Experiment 3. The error bars represent the within-participants standard errors of the means

conditions were consistent with those of a previous study with a fixation dot (L. E. Ross & Ross, 1980) and was explained in terms of the general warning effect, since the change of the fixation object was available as a temporal cue for the target onset. In contrast, the shift conditions yielded shorter latencies than the appearance conditions, although both conditions provided a temporal cue. Perhaps the delayed saccadic response of the appearance conditions relative to the shift conditions came from factors other than the general warning effect.

General discussion

In the present study, we demonstrated that the gaze direction (direct vs. averted) of the eyes of a fixated face differently affected saccadic latencies, but only in a particular situation. Experiment 1 showed that the gaze direction of the eyes had no influence on the subsequent saccadic responses in the ordinal gap-overlap paradigm-that is, when the eyes disappeared shortly before the target onset (gap condition) or remained present until the end of saccades (overlap condition). However, the saccadic latency was modulated when the gaze direction was directed toward or was averted from participants shortly before the target onset, in which case the appearance of eye contact resulted in a slower response than did the disappearance of eye contact. A control experiment regarding the geometric factors of the fixation stimulus (Exp. 2) ruled out the possibility that the differential vertical displacement of the fixated point (i.e., center to periphery vs. periphery to center) by itself caused the differential modulations. Experiment 3 revealed that the abrupt appearance of a direct and averted gaze prior to the target onset facilitated the subsequent saccade to different degrees. Thus, the crucial factor was the gaze direction of the fixation stimulus immediately before the saccades.

The main finding of the present study was that semantic changes as well as physical changes of the fixation stimulus, particularly the appearance and disappearance of eye contact, modulate saccadic facilitation in the target-elicited saccade paradigm. Specifically, the perception of another's direct gaze results in smaller response facilitation than does the perception of averted gaze. In a previous study, we demonstrated that the subjective interpretations of a fixation stimulus also affects the saccadic gap effect (Ueda et al., 2013). Thus, although the direct causes of gap facilitation are thought to be automatic processes such as fixation offset or attentional disengagement, our results suggest that these processes may interact with a wider range of processes than has previously been considered.

Eye contact is known to convey a wealth of nonverbal information, which is fundamental for social interactions and communications (Emery, 2000; Kleinke, 1986). Eye contact has been shown to affect our perceptual and cognitive processes, leading to a higher sensitivity to a direct gaze and to attentional capture by it. For instance, we are good at finding the direct gaze among averted gazes in the visual search paradigm, a phenomenon known as the *stare-in-the-crowd effect* (Conty et al., 2006; Doi & Ueda, 2007; Palanica & Itier, 2011; Senju et al., 2005; von Grünau & Anston, 1995). Yokoyama, Ishibashi, Hongoh, and Kita (2011) showed that a transition from averted to direct gaze captures visual spatial attention and facilitates subsequent target detection at the location of the directed gaze. Taken together, it may be possible to argue that, in the present experiments, more attentional resources were allocated to a facial stimulus with a directed gaze, and hence attentional release from the fixation was interfered with, resulting in longer saccadic latencies.

From the results of the present study, however, we do not dispute the involvement of processes other than attentional modulation. The facilitation of saccadic response in the gap effect is associated with the lower-level component-namely, the fixation offset effect. The gaze modulation observed here might also interact with lower-level processes, including the superior colliculus. Recent studies have shown that higher sensitivity to direct gaze is observed even in unconscious processes (Burra et al., 2013; Stein, Senju, Peelen, & Sterzer, 2011); thus, the process for eye contact is considered to be a rapid and implicit process (for reviews, see Johnson, 2005; Senju & Johnson, 2009). Furthermore, lesion studies have indicated that, in addition to saccadic execution (e.g., Dorris & Munoz, 1995; Munoz & Wurtz, 1992), the superior colliculus is also involved in relatively higher functions, such as target selection and selective attention (Goffart, Hafed, & Krauzlis, 2012; Lovejoy & Krauzlis, 2010; Song, Rafal, & McPeek, 2011). The involvement of the fixation offset effect and superior colliculus in the saccadic facilitation/inhibition by gaze directions needs to be directly addressed in future studies.

The present study also suggests that the temporal window of the influence of gaze direction on subsequent saccades is narrow; the appearance of the direct-gaze fixation yielded longer saccadic latencies only when a target was presented shortly (200 ms) after the onset of the direct-gaze fixation. The overlap conditions in Experiments 1 and 3 and the appearance condition in Experiment 3 were almost identical, except for the elapsed time between the onset of the directed gaze and the target. However, when the direct gaze appeared 1,000 ms before a target (i.e., overlap conditions), the influence of gaze direction was absent. On the other hand, when the direct gaze appeared 200 ms before a target (appearance and shift conditions), the gaze direction influenced subsequent saccades. Therefore, the present study demonstrated that a social signal (eye contact) affects the initiation of a subsequent saccade, but this influence is short lived and does not last longer than 1,000 ms. These results are consistent with a previous study that showed the influence of gaze direction on subsequent manual responses (Seniu & Hasegawa, 2005). Seniu and Hasegawa compared the effects of direct, averted, and no (i.e., closed-eye) gaze fixations in gap and overlap conditions and found that the reaction times of manual responses were longer after the presentation of the direct gaze than after the averted gaze. Importantly, the difference between the gaze directions was found only when the presentation duration of the face stimuli prior to the target onset was short (500 ms); a longer presentation duration (1,200 ms) nulled the effects. Thus, the influence of the social signal from gaze direction on the initiation of subsequent action seems to be short-lived, irrespective of the response modalities. The similar time courses for saccadic and manual reaction times are likely to be due to a common factor underlying the saccadic and manual gap effects (e.g., Pratt, Bekkering, Abrams, & Adam, 1999).

In summary, the results of the present study suggest that social signals from eye contact before target onset—specifically, the gaze direction of others—could potentially serve to change the initiation of the subsequent action.

Author note This work was supported by a Grant-in-Aid for Japan Society for the Promotion of Science (JSPS) Fellows (to H.U.), by Grants-in-Aid for Scientific Research (Nos. 24300279 and 23240034, to K.W., and 25700013, to K.T.) from the Ministry of Education, Culture, Sports, Science and Technology, and by CREST (to K.W.), JST, Japan.

References

- Bell, A. H., Meredith, M. A., Van Opstal, A. J., & Munoz, D. P. (2006). Stimulus intensity modifies saccadic reaction time and visual response latency in the superior colliculus. *Experimental Brain Research*, 174, 53–59.
- Boch, R., Fischer, B., & Ramsperger, E. (1984). Express-saccades of the monkey: Reaction times versus intensity, size, duration, and eccentricity of their targets. *Experimental Brain Research*, 55, 223–231.
- Brainard, D. H. (1997). The Psychophysics Toolbox. Spatial Vision, 10, 433–436. doi:10.1163/156856897X00357
- Burra, N., Hervais-Adelman, A., Kerzel, D., Tamietto, M., de Gelder, B., & Pegna, A. J. (2013). Amygdala activation for eye contact despite complete cortical blindness. *Journal of Neuroscience*, *33*, 10483– 10489. doi:10.1523/JNEUROSCI.3994-12.2013
- Conty, L., Tijus, C., Hugueville, L., Coelho, E., & George, N. (2006). Searching for asymmetries in the detection of gaze contact versus averted gaze under different head views: A behavioural study. *Spatial Vision*, 19, 529–545.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers,* 34, 613–617.
- Doi, H., & Ueda, K. (2007). Searching for a perceived stare in the crowd. Perception, 36, 773–780.
- Dorris, M. C., & Munoz, D. P. (1995). A neural correlate for the gap effect on saccadic reaction times in monkey. *Journal of Neurophysiology*, 73, 2558–2562.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience & Biobehavioral Reviews*, 24, 581–604.

- Fendrich, R., Hughes, H. C., & Reuter-Lorenz, P. A. (1991). Fixationpoint offsets reduce the latency of saccades to acoustic targets. *Perception & Psychophysics*, 50, 383–887.
- Fischer, B., & Ramsperger, E. (1984). Human express saccades: Extremely short reaction times of goal directed eye movements. *Experimental Brain Research*, 57, 191–195.
- Goffart, L., Hafed, Z. M., & Krauzlis, R. J. (2012). Visual fixation as equilibrium: Evidence from superior colliculus inactivation. *Journal* of Neuroscience, 32, 10627–10636.
- Jin, Z., & Reeves, A. (2009). Attentional release in the saccadic gap effect. Vision Research, 49, 2045–2055.
- Johnson, M. H. (2005). Subcortical face processing. Nature Reviews Neuroscience, 6, 766–774.
- Kalesnykas, R. P., & Hallett, P. E. (1987). The differentiation of visually guided and anticipatory saccades in gap and overlap paradigms. *Experimental Brain Research*, 68, 115–121.
- Kalesnykas, R. P., & Hallett, P. E. (1994). Retinal eccentricity and the latency of eye saccades. *Vision Research*, 34, 517–531.
- Kingstone, A., & Klein, R. M. (1993). Visual offsets facilitate saccadic latency: Does predisengagement of visuospatial attention mediate this gap effect? *Journal of Experimental Psychology*, 19, 1251– 1265.
- Kleinke, C. L. (1986). Gaze and eye contact: A research review. *Psychological Bulletin*, 100, 78–100.
- Lovejoy, L. P., & Krauzlis, R. J. (2010). Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nature Neuroscience*, 13, 261–266.
- Munoz, D. P., & Wurtz, R. H. (1992). Role of the rostral superior colliculus in active visual fixation and execution of express saccades. *Journal of Neurophysiology*, 67, 1000–1002.
- Palanica, A., & Itier, R. J. (2011). Searching for a perceived gaze direction using eye tracking. *Journal of Vision*, 11(2), 19. doi:10.1167/11.2.19. 1–13.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442. doi:10.1163/156856897X00366
- Pratt, J., Bekkering, H., Abrams, R. A., & Adam, J. (1999). The Gap effect for spatially oriented responses. *Acta Psychologica*, 102, 1–12.
- Pratt, J., Bekkering, H., & Leung, M. (2000). Estimating the components of the gap effect. *Experimental Brain Research*, 130, 258–263.
- Pratt, J., Lajonchere, C. M., & Abrams, R. A. (2006). Attentional modulation of the gap effect. *Vision Research*, 46, 2602–2607.

- Reuter-Lorenz, P. A., Hughes, H. C., & Fendrich, R. (1991). The reduction of saccadic latency by prior offset of the fixation point: An analysis of the gap effect. *Perception & Psychophysics*, 49, 167– 175.
- Ross, L. E., & Ross, S. M. (1980). Saccade latency and warning signals: Stimulus onset, offset, and change as warning events. *Perception & Psychophysics*, 27, 251–257.
- Ross, S. M., & Ross, L. E. (1981). Saccade latency and warning signals: Effects of auditory and visual stimulus onset and offset. *Perception* & *Psychophysics*, 29, 429–437.
- Saslow, M. G. (1967). Latency for saccadic eye movement. *Journal of the Optical Society of America*, 57, 1024–1029.
- Senju, A., & Hasegawa, T. (2005). Direct gaze captures visuospatial attention. Visual Cognition, 12, 127–144.
- Senju, A., Hasegawa, T., & Tojo, Y. (2005). Does perceived direct gaze boost detection in adults and children with and without autism? The stare-in-the-crowd effect revisited. *Visual Cognition*, 12, 1474– 1496.
- Senju, A., & Johnson, M. H. (2009). The eye contact effect: Mechanisms and development. *Trends in Cognitive Sciences*, 13, 127–134.
- Song, J.-H., Rafal, R. D., & McPeek, R. M. (2011). Deficits in reach target selection during inactivation of the midbrain superior colliculus. *Proceedings of the National Academy of Sciences*, 108, 1433–1440.
- Stein, T., Senju, A., Peelen, M. V., & Sterzer, P. (2011). Eye contact facilitates awareness of faces during interocular suppression. *Cognition*, 119, 307–311.
- Ueda, H., Takahashi, K., & Watanabe, K. (2013). Contributions of retinal input and phenomenal representation of a fixation object to the saccadic gap effect. *Vision Research*, 82C, 52–57.
- Vernet, M., Yang, Q., Gruselle, M., Trams, M., & Kapoula, Z. (2009). Switching between gap and overlap pro-saccades: Cost or benefit? *Experimental Brain Research*, 197, 49–58. doi:10.1007/s00221-009-1887-1
- von Grünau, M., & Anston, C. (1995). The detection of gaze direction: A stare-in-the-crowd effect. *Perception*, 24, 1297–1313.
- Walker, R., Kentridge, R. W., & Findlay, J. M. (1995). Independent contributions of the orienting of attention: Fixation offset and bilateral stimulation on human saccadic latencies. *Experimental Brain Research*, 103, 294–310.
- Yokoyama, T., Ishibashi, K., Hongoh, Y., & Kita, S. (2011). Attentional capture by change in direct gaze. *Perception*, 40, 785–797.