

博士論文

Effects of the physical and perceptual
representation of visual objects on
visuomotor responses

(視覚運動反応における高次物体表象の影響)

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Effects of the physical and perceptual representation of visual objects on visuomotor responses

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Abstract

The latency of target-elicited saccades and manual movements is facilitated by the removal of a fixation stimulus shortly before the target onset (i.e., the gap effect). The present study investigated the influence of perceptual as well as physical aspects of a fixation stimulus on the saccadic and manual gap effects. Study 1 (Chapter 2) showed that occlusion of a fixation stimulus prior to target onset produces only partial facilitation of saccadic responses and no facilitation of manual responses. Thus, both subjective representation and the physical inputs of a fixation stimulus affect subsequent saccadic and manual responses. Study 2 (Chapter 3) demonstrated that an interocularly suppressed (i.e., invisible) fixation stimulus influences saccadic responses but not manual responses. The results of these two studies confirm that the saccadic gap effect occurs only when the fixation stimulus disappears both physically and subjectively, whereas the manual gap effect is strongly correlated with the subjective representation of a fixation stimulus. Study 3 (Chapter 4) further demonstrated that even a higher cognitive function (i.e., perception of another person's gaze) interacts with the saccadic gap effect, but not with the manual gap effect. These results indicate that the saccadic and manual gap effects arise from at least partially different mechanisms. In particular, the saccadic gap effect is primarily mediated via fast and automatic subcortical processes although its magnitude is modulated by higher perceptual and cognitive functions. In contrast, the manual gap effect presumably depends more on higher cognitive processes.

Table of Contents

Acknowledgment	ii
Abstract	iii
Table of Contents	iv
List of Figures	vi
List of Tables.....	vii
Chapter 1: Introduction	1
1.1 Background	1
1.2 Objectives of the study.....	9
Chapter 2: Effects of the Physical Disappearance and Subjective Maintenance of a Fixation Stimulus on the Saccadic and Manual Gap Effects	15
2.1 Introduction	15
2.2 Experiment 1: Effects of an occluded fixation stimulus on the saccadic gap effect.....	17
2.3 Experiment 2: Effects of an occluded fixation stimulus on the manual gap effect.....	23
2.4 Experiment 3: Effects of phenomenal permanence and expectation of the reappearance of an occluded fixation stimulus on the saccadic gap effect.....	26
2.5 Experiment 4: Effects of phenomenal permanence and expectation of the reappearance of an occluded fixation stimulus on the manual gap effect.....	28
2.6 Control Experiment 1: Gradual vs. abrupt disappearance of the fixation stimulus	30
2.7 Control Experiment 2: Modulation of the general warning effect due to the possible reappearance of the occluded fixation stimulus	32
2.8 Control Experiment 3: Subjective impression of maintenance and reappearance of an occluded fixation stimulus	34
2.9 General discussion	37

Chapter 3: Effects of the Subjective Disappearance and Physical Maintenance of a Fixation Stimulus on the Saccadic and Manual Gap Effects	42
3.1 Introduction	42
3.2 Experiment 5: Effects of the disappearance and maintenance of an invisible fixation stimulus on the saccadic gap effect.....	46
3.3 Experiment 6: Effects of disappearance and maintenance of an invisible fixation stimulus on the manual gap effect	52
3.4 Control Experiment 4: Objective measures of the suppression effectiveness	55
3.5 General discussion	56
Chapter 4: Effects of Social Signals from a Gaze-Fixation Stimulus on the Saccadic and Manual Gap Effects.....	62
4.1 Introduction	62
4.2 Experiment 7: Effects of the disappearance and appearance of eye contact on saccadic responses.....	64
4.3 Experiment 8: Effects of the disappearance and appearance of eye contact on manual responses	70
4.4 Experiment 9: Effects of the geometric property of gaze shifts on saccadic responses	73
4.5 Experiment 10: Effects of the geometric property of gaze shifts on manual responses	77
4.6 Experiment 11: Effects of gaze shift from averted to direct vs. a sudden direct-gaze appearance on saccadic responses	80
4.7 General discussion	82
Chapter 5: Conclusion.....	88
References	94

List of Figures

Chapter 1

Figure 1. The gap effect	4
Figure 2. Amodal completion	10
Figure 3. Schematic illustration of the trial sequences in Experiment 1	21
Figure 4. Results of Experiment 1	23
Figure 5. Results of Experiment 2	25
Figure 6. Results of Experiment 3	28
Figure 7. Results of Experiment 4	30
Figure 8. Results of Control Experiment 3	37

Chapter 3

Figure 9. Binocular rivalry and continuous flash suppression	44
Figure 10. Schematic illustration of the trial sequences in Experiment 5	50
Figure 11. Results of Experiment 5	52
Figure 12. Results of Experiment 6	55

Chapter 4

Figure 13. Schematic illustration of the trial sequences in Experiment 7	67
Figure 14. Results of Experiment 7	69
Figure 15. Results of Experiment 8	72
Figure 16. Schematic illustration of the trial sequences in Experiment 9	74
Figure 17. Results of Experiment 9	76
Figure 18. Results of Experiment 10	79
Figure 19. Schematic illustration of the trial sequences in Experiment 11	81
Figure 20. Results of Experiment 11	82

List of Tables

Chapter 4

Table 1. Results of Experiment 7	69
Table 2. Results of Experiment 8	72
Table 3. Results of Experiment 9	77
Table 4. Results of Experiment 10	80

CHAPTER

1

Introduction

1.1 BACKGROUND

High visual acuity in the human eye is restricted to a small region in the central retina called the fovea, and it drops significantly with increasing distance between the perceived image and the fovea. Because the fovea only represents approximately 1° of the visual angle, people continually need to move their eyes back and forth in order to bring the area of visual interest into focus (i.e., the process of foveation). Thus, it seems that the visual world is constructed through eye movements. The importance of eye movements in vision has made their study an active area of research. As a result, there have been extensive studies investigating the mechanisms of a process called saccade, or the way in which visual orientation is achieved by moving eye gaze from one location to another. Because time is a critical factor when one is attempting to efficiently scan the visual field for information, the reaction time (or latency) of orienting saccades from a previously fixed location to a new location has been intensively studied.

In a typical experimental setting, the saccadic latency is studied using a target-elicited saccade paradigm. Observers are asked to keep their eyes on an initial fixation location, usually at the center of the visual field, and to move their eyes toward a target when it appears, typically at the periphery of the visual field. Among the determinants of saccadic latency in this task are the properties of the target stimulus, such as intensity and location. For instance, a bright target stimulus is known to induce a faster saccadic reaction time than is 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. Neurophysiological studies have shown some support for this hypothesis at the level of neuronal activity, particularly in the superior colliculus (SC) of monkeys (Bell, Meredith, Van Opstal, & Munoz, 2006). Two aspects of the target's location also affect saccadic latency in the target-elicited paradigm: the distance (i.e., retinal eccentricity) and relative direction from the initial fixation stimulus. The saccadic latency is relatively shorter with a target eccentricity between approximately 1° and 10° , and it increases with smaller ($< 1^\circ$) or larger ($>10^\circ$) eccentricities (Kalesnykas & Hallett, 1994); where the eccentricities larger than 20° requires both eye and head movements (termed a head field in contrast to a eye field) and those larger than 90° requires additional body movements. In addition, the saccadic latency tends to be shorter when the target is presented in a horizontal direction than when it is presented in a vertical direction relative to the initial fixation stimulus (Vernet, Yang, Gruselle, Trams, & Kapoula, 2009).

The influence of target properties on saccadic latency in this paradigm is rather intuitive. Surprisingly, however, the properties of the initial fixation stimulus have a larger influence on 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 (see “gap condition” in the top panel of Figure 1), the saccadic response to the target is faster than if the fixation stimulus remained present (see “overlap condition” in the bottom panel of Figure 1). This phenomenon was first reported by Saslow (1967) and is termed the “gap effect” because there is a blank screen (i.e., gap) between the fixation offset and the target onset (e.g., Dorris & Munoz, 1995; Fischer & Ramsperger, 1984; Kalesnykas & Hallett, 1987; Kingstone & Klein, 1993; Reuter-Lorenz et al., 1991).

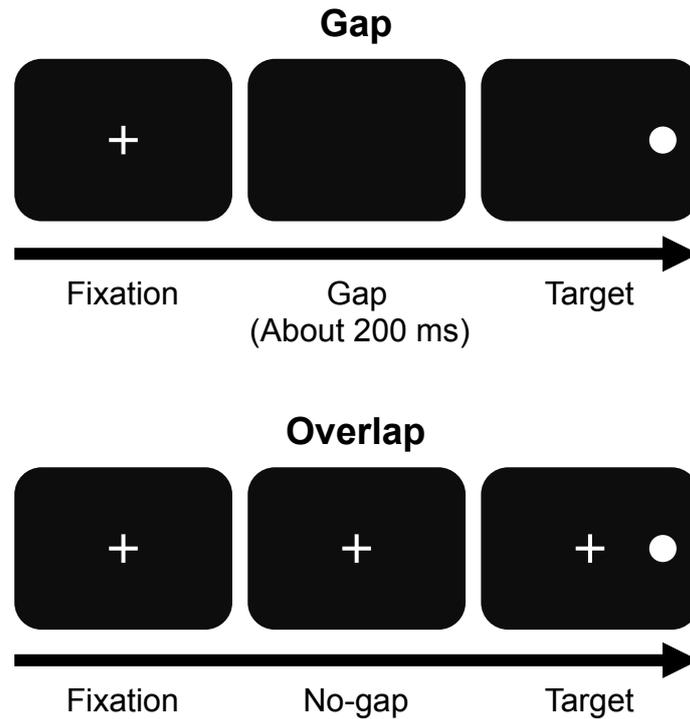


Figure 1. The gap effect. The reduction of a saccadic latency to a peripherally presented target (dot) when the fixation stimulus (plus) disappears shortly before the target onset (i.e., the gap condition: *top*) as compared to when the fixation stimulus remains present (i.e., the overlap condition: *bottom*).

The gap effect is a robust phenomenon. The gap effect 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), and its magnitude (i.e., the degree of the reduction in reaction time) sometimes can reach 100 ms. In addition, the gap effect has been observed in people with a wide range of ages (Fischer et al., 1993; Munoz, Broughton, Goldring, & Armstrong, 1998; Vernet et al., 2009) and in non-human primates (Dorris & Munoz, 1995; Fischer & Boch, 1983; Kano, Hirata, Call, & Tomonaga, 2011).

The gap effect's distinguishing feature is that its facilitating effect strongly depends on the "disappearance" of the previously attended fixation stimulus. Because the fixation offset always precedes the target onset, this can serve as a temporal cue that induces motor preparation for the subsequent response, and results in a quicker reaction time to the target (termed the *warning effect*; Kingstone & Klein, 1993; Reuter-Lorenz et al., 1991; L. E. Ross & Ross, 1980; S. M. Ross & Ross, 1981). The warning effect has been observed under a variety of conditions, including physical changes to the fixation stimulus (e.g., size, luminance, color), onset/offset of the fixation stimulus, or presentation of an auditory signal preceding the target presentation (Jin & Reeves, 2009; Pratt, Bekkering, & Leung, 2000; L. E. Ross & Ross, 1980; S. M. Ross & Ross, 1981). For this reason, it has become known as the *general warning effect*, and is considered the primary component of the *manual gap effect* (Jin & Reeves, 2009; Kingstone & Klein, 1993; see also below). However, the warning effect does not fully explain the mechanism underlying the saccadic gap effect. For example, among several tested warning signals, the disappearance of the fixation stimulus (i.e., the "classic" gap condition) always caused the largest response facilitation (Jin & Reeves, 2009; Pratt et al., 2000). Therefore, although the general warning effect can account for the saccadic gap effect, it plays only a minor role, and there remains an unexplained effect of the disappearance of the fixation stimulus for expediting the subsequent target-elicited saccade.

Although various theories have been postulated regarding the fixation-offset-specific component of the gap effect, two are considered primary (see Jin & Reeves, 2009, for a review). The first is the *fixation offset effect* (e.g., Fendrich, Hughes, & Reuter-Lorenz, 1991; Kingstone & Klein, 1993; Munoz & Wurtz, 1992; Reuter-Lorenz et al., 1991), which involves oculomotor release from active fixation processes, and the second is *attentional predisengagement theory* (e.g., Fischer & Breitmeyer, 1987; Fischer & Weber, 1993; Jin & Reeves, 2009; Mackeben & Nakayama, 1993; Pratt et al., 2000; Pratt, Lajonchere, & Abrams, 2006), which involves predisengagement of spatial attention from the attended fixation location.

Kingstone & Klein (1993) have postulated that the saccadic gap effect is primarily caused by the oculomotor-specific fixation offset effect combined with a motor preparation triggered by the general warning effect. The fixation offset effect assumes that the maintenance of fixation interferes with the plan or execution of a subsequent saccadic movement at the oculomotor level, and the removal of the visual inputs of the fixation stimulus overcomes this interference and hence facilitates the subsequent saccade initiation. Neural substrates of these processes have been found in the SC of non-human primates (e.g., Dorris & Munoz, 1995; Munoz & Wurtz, 1992, 1993a). In particular, there is some evidence that a fixation process is associated with the activation of “fixation cells” in the rostral pole of the SC, and that activation inhibits the activation of the saccade generating “movement cells” in the intermediate layer of the SC. In other words, according to the fixation offset effect, the saccadic gap effect occurs

because the disappearance of the fixation stimulus reduces activity in the fixation cells, which consequently disinhibits the activity of the movement cells and allows a quicker saccadic initiation to the target when it appears; otherwise, the release process takes place only after the appearance of the target.

While the fixation offset effect interprets the saccadic gap effect as a relatively lower automatic phenomenon, the attentional predisengagement theory postulates that a relatively higher cortical mechanism, covert attentional orienting, plays a significant role in the gap effect. This theory is based on Posner's attention orienting theory (Posner, 1980), which states that orienting attention to a new location requires disengagement of attention from the currently attended location. Therefore, the attentional predisengagement theory assumes that disappearance of the fixation stimulus before the target onset allows disengagement of attention from the fixation location because it assumes that (1) there is a strong coupling between attention and saccades, and (2) an attentional shift always precedes a saccade. This results in an immediate attentional and subsequent saccadic shift; otherwise, the disengagement of attention takes place only after the target onset and with the fixation stimulus remaining present. Several behavioral studies have indicated that attention is involved in the saccadic gap effect. For example, Pratt et al. (2006) have shown that removal of an attended portion of a fixation stimulus induces a larger gap effect than does removal of an unattended portion of the stimulus. An indirect measure of attentional state during the gap-overlap task (Jin & Reeves, 2009) has also indicated that attentional release begins approximately 80 ms

after the fixation period ends. In addition, greater attentional release occurred in the gap condition than in an overlap condition, in which manual reaction times to a probe dot appearing at different times were measured during a gap-overlap task.

Therefore, while the fixation offset effect assumes involvement of oculomotor-specific automatic components, the attentional predisengagement theory assumes involvement of an attention-related perceptual component. Although there is substantial evidence in support of both theories, a consensus in the literature has not yet been reached. In other words, these two models are not necessarily mutually exclusive.

In addition to the saccadic gap effect, several studies have reported that response facilitation in the gap paradigm also occurs to manual movements, such as pointing and key-pressing (i.e., the *manual gap effect*; Bekkering, Pratt, & Abrams, 1996; Jin & Reeves, 2009; Pratt, Bekkering, Abrams, & Adam, 1999; Song & Nakayama, 2007). One of the major questions regarding the manual gap effect is whether the observed response facilitation arises from or shares the same underlying mechanism as the saccadic gap effect. In contrast to the saccadic gap effect, several studies have indicated that the primary component of the manual gap effect is the general warning effect (Jin & Reeves, 2009; Kingstone & Klein, 1993; Reuter-Lorenz et al., 1991; Tam & Ono, 1994). Indeed, all previous studies of the saccadic and manual gap effects have shown greater response facilitation in saccadic responses than manual responses. Moreover, some studies have not shown any response facilitation in manual responses when the effect of the warning signal was fully controlled. (Reuter-Lorenz et al., 1991; Tam &

Ono, 1994). Furthermore, lack of interference between the saccadic and manual reaction times in a dual task (i.e., making a saccade and manual movement in the same task) indicates that those two facilitation effects are mediated by two different mechanisms (Jin & Reeves, 2009), though they may share similarities (e.g., the relation between the magnitude of the facilitation and the length of the gap period; Pratt et al., 1999).

1.2 OBJECTIVES OF THE STUDY

Although the fixation offset effect and attentional predisengagement theory assume that neuronal mechanisms operating at different levels (i.e., subcortical and cortical mechanisms, respectively) are responsible for the generation of the gap effect, both posit that the facilitation of saccadic responses is attributed to the disappearance of the fixation stimulus prior to target presentation. Thus, previous studies on the gap effect have focused on the disappearance and maintenance of the physical visual inputs of a fixation stimulus on the retina. Human perceptual or subjective experience, however, does not necessarily reflect the physical inputs to the retina. For instance, in daily life, the physical inputs of an attended object on the retina are often disrupted by the inputs of other objects, but our perceptual experience does not lose the spatiotemporal continuity of the attended object, a phenomenon called amodal completion (see Figure 2).

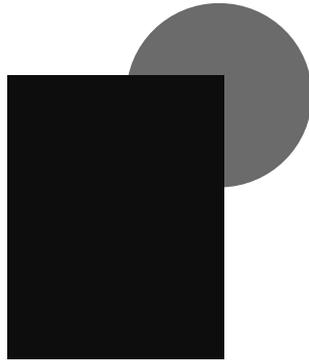


Figure 2. Amodal completion. The perceptual completion of an object when the physical sensory inputs of the object are missing, such as due to partial occlusion of the object.

The objective of this study was to investigate the contributions of the subjective and physical properties of the disappearance and maintenance of the fixation stimulus in the gap effect. Toward that aim, a series of experiments was conducted using visual perceptual phenomena in which the physical inputs and perceptual representation of a fixation stimulus were separable.

Study 1 (Chapter 2) examined the contribution of perceptual representation or the subjective disappearance and maintenance of a fixation stimulus to the gap effect. This condition was achieved by using the phenomenal permanence and the tunnel effect of an occluded fixation stimulus, which may be better known as the amodal completion (Burke, 1952; Gibson, Kaplan, Reynolds, & Wheeler, 1969; Michotte, 1950). In other words, with this manipulation, observers perceived the occlusion of a fixation stimulus, which gave the subjective impression that the fixation stimulus was maintained while the physical inputs disappeared. In Study 2 (Chapter 3), the contribution of the physical disappearance and maintenance of a fixation stimulus was examined while

independently manipulating the subjective disappearance and maintenance of the fixation stimulus. For this purpose, the visibility of a fixation stimulus was manipulated by using binocular rivalry (for reviews, see Blake & Logothetis, 2002; Lin & He, 2009) and the continuous flash suppression (CFS) technique (Tsuchiya & Koch, 2005), in which a series of rapidly changing dynamic stimuli is presented to one eye such that the static stimuli on the other eye are rendered invisible. Thus, in Study 2, the disappearance and maintenance of a visible and an invisible fixation stimulus were manipulated independently to dissociate the physical inputs of a fixation stimulus from its subjective representation.

The results of the present study will have significant relevance for the predominant theories of the gap effect. In short, the current view on the gap effect assumes that response facilitation consists of two major components: the general warning effect and the specific component(s) of fixation offset. The trigger of the general warning effect is not necessarily the offset of the fixation stimulus, but may be anything that serves as a temporal cue for target onset, such as onset of the fixation stimulus. The contribution of the general warning effect to the gap effect for both saccade and manual responses is relatively widely accepted. However, the component(s) specific to the disappearance of the fixation stimulus, especially regarding the relation between the fixation offset effect and attentional predisengagement theory, has not yet reached a consensus. The major advantage of the paradigm used in the present studies is that separation of the contributions of the physical and the subjective disappearance of the fixation stimulus

allows elucidating the roles of oculomotor-specific fixation offset and attentional disengagement in the gap effect. In general, the major difference between the fixation offset effect and the attentional predisengagement theory is that they attribute the origin of the gap effect to the different levels of neural mechanisms, namely subcortical and cortical processes, respectively. In other words, the fixation offset effect attributes the main cause of the gap effect to the physical disappearance of the fixation stimulus, whereas the attentional predisengagement theory assumes that the gap effect occurs as long as attentional disengagement from the fixation location successfully occurs. Hence, the physical disappearance of the fixation stimulus would be sufficient to cause the gap effect for the former theory, whereas the subjective disappearance of the fixation stimulus would be sufficient for the latter theory. Therefore, revealing the contributions of the physical and subjective disappearance of the fixation stimulus will confirm/disconfirm these hypotheses.

Another interest of the present study is to investigate whether the saccadic and manual gap effects share underlying mechanisms, especially regarding cortical and subcortical processes. Unlike the saccadic gap effect, which is considered to be mediated primarily by the subcortical oculomotor system (e.g., the fixation offset effect), the manual gap effect is more likely to depend on cortical mechanisms. Bekkering et al. (1996) showed that while saccadic responses involve more reflexive processes, manual responses involve more decisional processes, though this may be restricted to selective movements but not to direct pointing and reaching movements to the target (Abekawa

& Gomi, 2010; Gomi, Abekawa, & Nishida, 2006; Gomi, Abekawa, & Shimojo, 2013). In particular, the manual gap effect has been observed only in a choice reaction task (i.e., pressing one of two keys according to a target position), but not in a simple reaction task (i.e., pressing a single key regardless of a target position). Friesen and Kingstone (2003) have also demonstrated that gaze direction cues (i.e., central endogenous cues) in a gap condition influence only manual responses but not saccadic responses; manual reactions were facilitated or inhibited depending of the validity of the gaze cues, whereas saccade reactions were facilitated by the offset of the gazing face without any influence from gaze-direction cues. Furthermore, studies on inhibition of return (IOR; i.e., increased reaction times to a previously cued and/or attended location; (Posner et al., 1985), which is often compared with the gap effect, have indicated that manual and ocular IOR may originate from different processes. The manual IOR results from inhibition of attentional orienting while the ocular IOR results from inhibition of motor preparation (Hunt & Kingstone, 2003; but see also Abrams & Dobkin, 1994; Souto & Kerzel, 2009). Given these findings, it is expected that the physical and perceptual disappearance and maintenance of the fixation stimulus differentially affect saccadic and manual gap effects. More specifically, the saccadic gap effect should have a greater dependence on the physical inputs of a fixation stimulus, whereas the manual gap effect should have a greater dependence on the perceptual representation of a fixation stimulus.

Study 3 (Chapter 4) examined how a higher cognitive function, gaze perception, interacts with the saccadic and manual responses in the gap-overlap paradigm. Although the physical differences in the visual images between direct and averted gazes are subtle, direct gaze (i.e., eye contact) from others seems to have special implications as a social signal (for reviews, see Emery, 2000; Senju & Johnson, 2009). For instance, several studies have reported that people are highly sensitive to direct gazes from others; in a visual search paradigm, it has been shown that detecting a direct gaze among averted-gaze distractors is faster than detecting an averted gaze among direct-gaze distractors (Conty, Tijus, Hugueville, Coelho, & George, 2006; Doi & Ueda, 2007; Palanica & Itier, 2011; Senju, Hasegawa, & Tojo, 2005; von Grünau & Anston, 1995). Furthermore, Senju and Hasegawa (2005) have demonstrated that shifting gaze from fixated eyes takes longer if the direction of the eyes is toward the observer rather than away from the observer. Therefore, the Study 3 aimed to elucidate how this cognitive-function-dependent factor modulates response facilitation in the gap effect. More specifically, I examined whether a change in the state of eye contact (i.e., breaking vs. making eye contact) of a cartoon fixation stimulus influences the gap effect. This study investigates the relation between the gap-overlap paradigm and facial fixation, a combination that is often used in the areas of developmental, clinical, and experimental psychology. Thus, the results of this study will have significant relevance in a broad range of areas, including developmental disorders, aging, and social interaction, as well as relevance to the study of the gap effect.

CHAPTER

2

Effects of the Physical Disappearance and Subjective Maintenance of a Fixation Stimulus on the Saccadic and Manual Gap Effects

2.1 INTRODUCTION

Previous studies of the gap effect have focused on the relation between the physical changes to the fixation stimulus and their consequent results on reaction time to the target. However, as seen in amodal completion, changes in the retinal signals of a visual stimulus are not always reflected in the subjective representation of the visual stimulus. In daily life, amodal completion often occurs when an attended object is occluded by another moving object, and vice versa. This gradual occlusion of visual stimuli is known to induce strong *phenomenal permanence*, which refers to the experience of the spatiotemporal continuity of an object even when physical inputs are no longer available (Gibson et al., 1969; Michotte, 1950), and the *tunnel effect* (Burke, 1952), which refers to the impression that the same object will reappear from behind the

occluder. Phenomenal permanence and the tunnel effect provide an interesting case in which physical inputs and subjective representation of a visual stimulus differ. Study 1 took advantage of this characteristic and tested whether the top-down components (i.e., the subjective impression of the maintenance and reappearance of a fixation stimulus), as well as stimulus-driven bottom-up components (i.e., the physical disappearance and maintenance of a fixation stimulus), influence the saccadic and manual gap effects.

The main objective of this study was to determine if higher cortical mechanisms (rather than subcortical mechanisms) are responsible for the gap effect. In other words, I examined whether the physical disappearance of a fixation stimulus is sufficient to cause the gap effect, regardless of the subjective maintenance or reappearance of that fixation stimulus. Thus, the fixation stimulus was covered by a moving mask 200 ms before target onset. With this manipulation, observers should think the fixation point is still present behind the mask even though inputs to the retina physically disappear because of the mask. The main advantage of this paradigm is that there are no extra task requirements as compared to the classic gap task described above. In other words, this paradigm can dissociate the endogenous component (e.g., attentional predisengagement) of the gap effect from the exogenous component (e.g., fixation offset) without increasing the difficulty of the task. Evidence that the endogenous component accounts for the gap effect will be obtained if the magnitude of response facilitation by the occluded fixation point is different from that of the disappeared fixation point, because the only difference between conditions is the perceptual representation of the fixation.

Alternatively, evidence for the exogenous component will be obtained if the magnitude of response facilitation by the occluded fixation point is comparable to that of the disappeared fixation point. Thus, Study 1 examined whether the phenomenal permanence of a temporary occluded fixation stimulus delays subsequent responses compared to a situation in which the fixation stimulus disappeared without occlusion.

2.2 EXPERIMENT 1: EFFECTS OF AN OCCLUDED FIXATION STIMULUS ON THE SACCADIC GAP EFFECT

In Experiment 1, the gradual occlusion method was used to investigate whether the phenomenal permanence of a fixation stimulus influences the saccadic gap effect. More specifically, the difference in saccadic reactions following the removal of a fixation stimulus with and without occlusion was examined.

Methods

Participants

Ten paid volunteers (four men and six women, aged 19–25 years) participated in the experiment. All had normal or corrected-to-normal vision and normal oculomotor function. All participants gave written informed consent before participation.

Experimental setup and apparatus

The experiment was conducted in a dark room. A chinrest was used to stabilize participants' head at a viewing distance of 56 cm. Visual stimuli were generated by

MATLAB (MathWorks), using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997), and were presented on a 21-inch CRT monitor with a refresh rate of 100 Hz. Eye movements were recorded with a desktop mounted EyeLink 1000 (SR Research) using the EyeLink Toolbox extensions (Cornelissen, Peters, & Palmer, 2002) of MATLAB.

Stimuli

The visual stimuli (see Figure 3a) consisted of a white fixation dot (0.32° in diameter, 43.0 cd/m^2), a white target dot (identical to the fixation stimulus), and black rectangular plates (i.e., occluders: $3.2^\circ \times 1.6^\circ$, 21.6 cd/m^2). The fixation stimulus was presented on the center of the screen, and the target stimulus was presented 4.0° to the left or right of the fixation stimulus. The black rectangular plates were vertically aligned along the center of the screen. The plates were separated by 1.8° and moved smoothly upward ($6.4^\circ/\text{sec}$) until the target dot was presented. All the stimuli were presented within a gray window ($12.0^\circ \times 9.0^\circ$, 32.4 cd/m^2).

Procedure

Each trial began with the presentation of the central fixation stimulus and the vertically moving rectangular plates (see Figure 3). The participants were required to keep their gaze on the central fixation stimulus. The target stimulus was equally likely to appear to the left or to the right of the fixation location. The participants were asked to respond to the target as quickly and as accurately as possible by directing their gaze

to the target location. The target stimulus remained on the screen for 1000 ms. Trials were separated by a 1000-ms inter-trial interval that was indicated by a tone.

Three conditions were tested: gap, occlusion, and overlap. The moving plates were passed either behind (gap and overlap conditions) or over (occlusion condition) the fixation stimulus. Thus, the fixation stimulus was visible during the fixation period in the gap and overlap conditions, but it was hidden in the occlusion condition. In all conditions, the fixation period continued until the 4th, 5th, or 6th plate had completely overlapped the fixation stimulus. The number of plates that passed across the fixation stimulus before target presentation was randomized for each trial. In the gap condition, the fixation stimulus was removed at the end of the fixation period (i.e., when the fixation stimulus was entirely enclosed by the last plate). In the overlap condition, the fixation stimulus remained in front of the plate. In the occlusion condition, the fixation stimulus was behind the plates. Then, following a period of 200 ms, the plates stopped moving and the target stimulus appeared.

The experiment consisted of 8 practice and 120 test trials in which the three testing conditions were intermixed and presented in a random order. Before the experiment, the eye tracker was calibrated using 12 reference points. Drift correction was also performed every 30 trials.

Data acquisition

Eye movements were recorded at a sampling rate of 250 Hz. The saccadic reaction time (SRT) was defined as the time from target onset to a saccade onset. The saccade onset was defined as the time at which the eye movement velocity exceeded a threshold of 30°/s.

Trials with SRTs less than 120 ms—that is, trials for which the mean correct response rate of 10 ms was less than the chance level (a one-tailed binomial test against 0.5, $p < 0.05$)—were regarded as being the result of anticipatory responses; thus, those trials were excluded from further analyses. Trials with SRTs greater than 3 σ from the mean on a log scale (529 ms) were also excluded because a lack of participant alertness was assumed. 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. Using these criteria, 3% of trials were removed from the analysis.

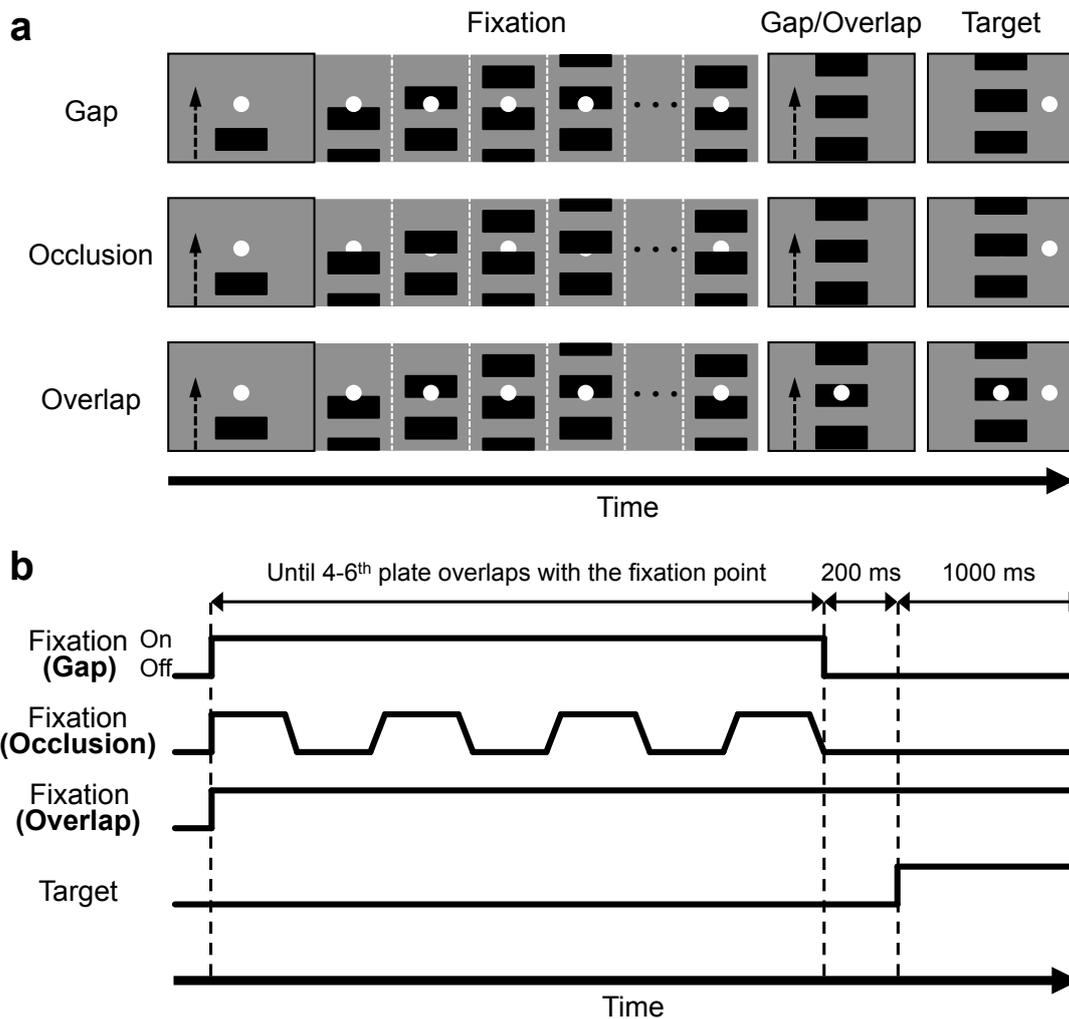


Figure 3. Schematic illustration of the trial sequences (a) and timelines (b) in Experiment 1. Each trial started with the presentation of a fixation stimulus while moving plates were passing behind (gap and overlap conditions) or over (occlusion conditions) the fixation stimulus. A fixation period lasted until 4–6 plates had completely overlapped the fixation stimulus. After the fixation period, the fixation stimulus disappeared (gap condition), was hidden by the moving plate (occlusion condition), or remained in front of the moving plate (overlap condition). Then, 200 ms later, the moving plates stopped and a target stimulus appeared at the left or right of the fixation location.

Results and Discussion

Figure 4 depicts the results of Experiment 1. The mean SRTs for the gap, occlusion, and overlap conditions were 198 ms, 243 ms, and 286 ms, respectively. A repeated measures ANOVA showed a significant main effect of fixation condition ($F(2,18) = 47.67, p < 0.001$). Post-hoc pairwise comparisons with a Bonferroni correction revealed that the SRTs were significantly different for all combinations ($p < 0.001$).

These results indicate that the removal of the retinal inputs of a fixated object facilitates saccadic response to a subsequently presented target, thus replicating the original gap effect. Furthermore, the results demonstrate that the gap effect is significantly reduced when the removal of the fixation stimulus was due to occlusion by other stimuli. However, the SRT following occlusion was still shorter compared to conditions in which the fixation stimulus was maintained in terms of both retinal input and phenomenal representation. Thus, the results of Experiment 1 suggest that physical as well as subjective disappearance and maintenance of a fixation stimulus influences the initiation of the subsequent saccade in the gap paradigm.

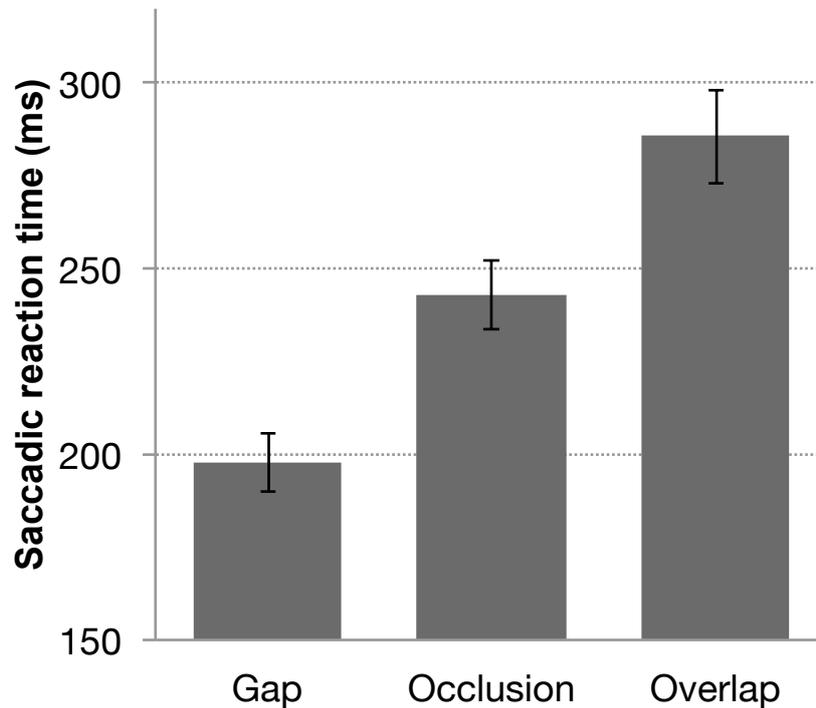


Figure 4. Mean SRTs in Experiment 1. Error bars represent the between-subject standard error of the mean.

2.3 EXPERIMENT 2: EFFECTS OF AN OCCLUDED FIXATION STIMULUS ON THE MANUAL GAP EFFECT

In Experiment 2, the same stimuli as in Experiment 1 were used to investigate whether the phenomenal permanence of a fixation stimulus influences the manual gap effect. The aim of this experiment was to highlight the similarities and differences between the manual and saccadic gap effects, especially regarding their dependency on the subjective information of visual stimuli.

Methods

Ten new paid volunteers (five men and five women, aged 18–24 years) participated in the experiment. All had normal or corrected-to-normal vision and normal eye-hand coordination. They all gave written informed consent prior to participation.

The stimuli and procedures were identical to those used in Experiment 1, except that participants were instructed to respond as quickly and accurately as possible to the target by pressing the corresponding left or right arrow key on the keyboard.

The manual reaction time (MRT) was defined as the time from the target onset to a key press. Trials with MRTs shorter than 250 ms or longer than 737 ms and with incorrect responses were excluded from data analysis (see Methods of Experiment 1 [Section 2.2] for a detailed description of the cut-off criteria). These criteria resulted in the removal of 3% of trials from the analysis.

Results and Discussion

The results of Experiment 2 are depicted in Figure 5. The mean MRTs for the gap, occlusion, and overlap conditions were 360 ms, 399 ms, and 406 ms, respectively. A repeated measures ANOVA revealed a significant main effect of fixation condition was significant ($F(2,18) = 32.00, p < 0.001$). Pairwise comparisons revealed that the MRT was significantly different between the gap and occlusion conditions ($p < 0.001$) and between the gap and overlap conditions ($p < 0.001$), but not between the occlusion and overlap conditions ($p = 0.26$).

Surprisingly, these results demonstrate that, unlike the saccadic gap effect, the manual gap effect is not induced by the disappearance of the physical inputs of the fixation point. Rather, the manual gap effect is solely based on the subjective disappearance of the fixation point. Thus, these results indicate that subjective representation of visual information, rather than retinal inputs, plays a significant role in the manual gap effect.

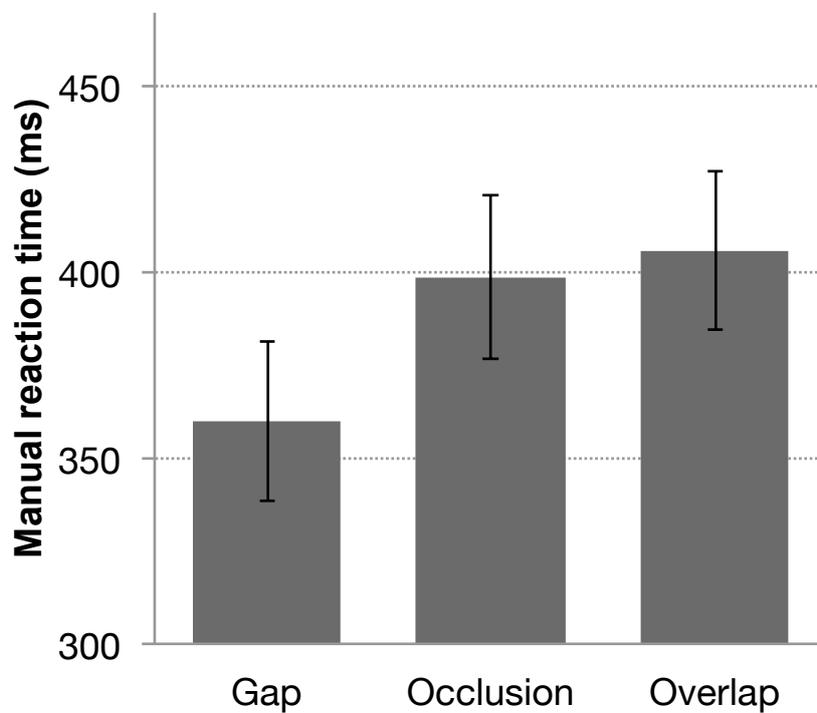


Figure 5. Mean MRTs in Experiment 2. Error bars represent the between-subject standard error of the mean.

2.4 EXPERIMENT 3: EFFECTS OF PHENOMENAL PERMANENCE AND EXPECTATION OF THE REAPPEARANCE OF AN OCCLUDED FIXATION STIMULUS ON THE SACCADIC GAP EFFECT

The occlusion condition in Experiment 1 leaves open the possibility that an expectation of the reappearance of the occluded fixation stimulus, as well as phenomenal permanence, affects the SRT. Thus, Experiment 3 examined whether phenomenal permanence was the cause of the observed delayed saccadic response. The occlusion condition was modified such that the color of the rectangular plates was the same as that of the background, inducing the experience of re-emergence of the fixation stimulus without phenomenal permanence; for the sake of clarity, this condition was called *pseudo-occlusion* in the present experiment.

Methods

Ten new paid volunteers (seven men and three women, aged 19–24 years) participated in the experiment. All had normal or corrected-to-normal vision and normal oculomotor function. They gave written informed consent prior to participation.

The same stimuli and procedures as Experiment 1 were used, except that the color of the rectangular plates was identical to that of the background.

Results and Discussion

The results of Experiment 3 are depicted in Figure 6. The mean SRTs for the gap, pseudo-occlusion, and overlap conditions were 200 ms, 235 ms, and 281 ms, respectively. A repeated measures ANOVA showed a significant main effect of fixation condition ($F(2,18) = 42.54, p < 0.001$). Pairwise comparisons also showed that the SRTs were significantly different across all conditions ($p < 0.005$).

An additional two-way mixed ANOVA with occluder type (visible vs. invisible) and fixation condition (gap vs. pseudo-occlusion vs. overlap) as factors was also performed to compare the results of Experiments 1 and 3. A significant main effect was found only for fixation condition ($F(2,36) = 90.00, p < 0.001$). Neither the main effect of occlusion type ($F(1,18) = 0.10, p = 0.75$) nor the interaction ($F(2,36) = 0.35, p = 0.70$) was significant. These results suggest that the expectation of the re-emergence of the fixation stimulus caused the weakened saccadic gap effect in the occlusion condition of Experiment 1, and that the effect of phenomenal permanence of a fixation stimulus was negligible.

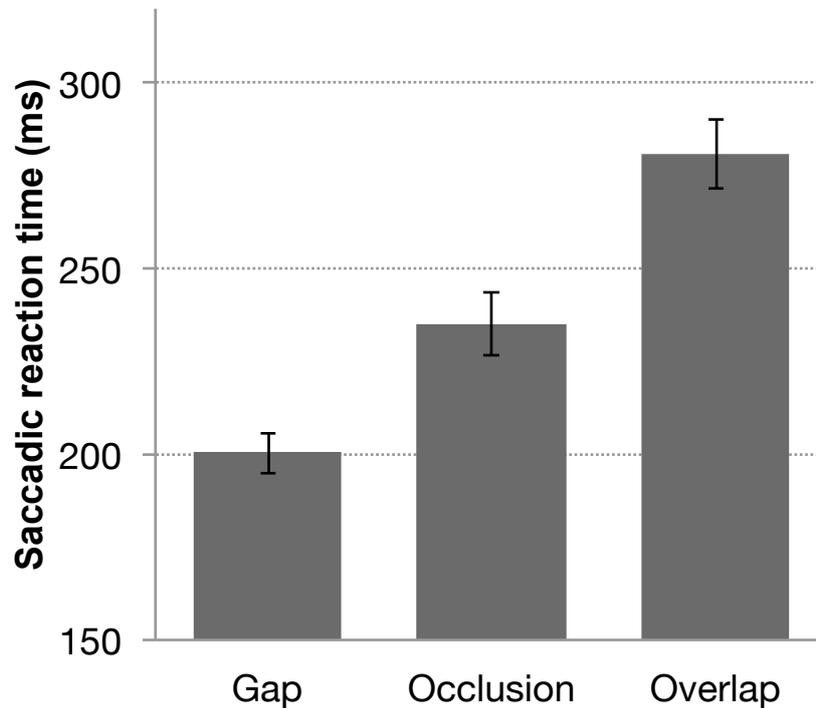


Figure 6. Mean SRTs in Experiment 3. Error bars represent the between-subject standard error of the mean.

2.5 EXPERIMENT 4: EFFECTS OF PHENOMENAL PERMANENCE AND EXPECTATION OF THE REAPPEARANCE OF AN OCCLUDED FIXATION STIMULUS ON THE MANUAL GAP EFFECT

In Experiment 4, the same stimuli as Experiment 3 were used to test whether phenomenal permanence or the expectation of the reappearance of a fixation stimulus inhibited the manual gap effect observed in the Experiment 2.

Methods

Ten new paid volunteers (seven men and three women, aged 20–24 years) participated in the experiment. All had normal or corrected-to-normal vision and normal eye-hand coordination. They gave written informed consent prior to participation. The stimuli and procedures were identical to those used in Experiment 3, except that the participants responded to the target by pressing an arrow key on the keyboard.

Results and Discussion

Figure 7 depicts the results of Experiment 4. The mean MRTs for the gap, pseudo-occlusion, and overlap conditions were 352 ms, 383 ms, and 390 ms, respectively. A repeated measures ANOVA indicated a significant main effect of fixation condition ($F(2,18) = 23.25, p < 0.001$). Pairwise comparisons showed that the MRTs were significantly different between the gap and pseudo-occlusion conditions ($p < 0.001$) and the gap and overlap conditions ($p < 0.001$), but not between the pseudo-occlusion and overlap conditions ($p = 0.30$).

An additional two-way mixed ANOVA with occluder type (visible vs. invisible) and fixation condition (gap vs. pseudo-occlusion vs. overlap) as factors indicated a significant main effect of fixation condition ($F(2,36) = 55.03, p < 0.001$). Neither the main effect of occlusion type ($F(1,18) = 0.28, p = 0.60$) nor the interaction ($F(2,36) = 0.53, p = 0.59$) was significant. These results indicate that the expectation of the

reappearance of a fixation stimulus rather than phenomenal permanence eliminated the manual gap effect observed in Experiment 2.

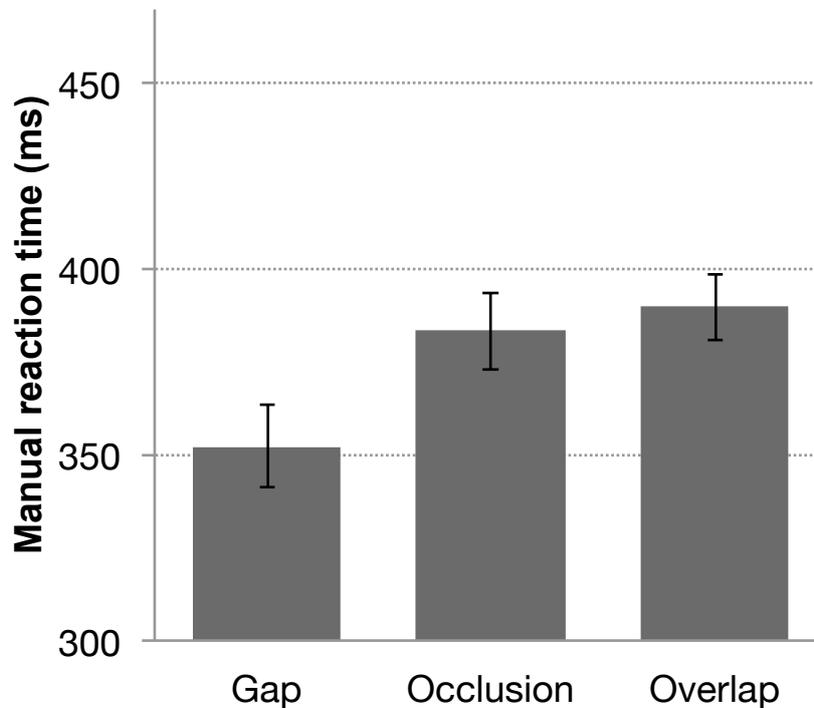


Figure 7. Mean MRTs in Experiment 4. Error bars represent the between-subject standard error of the mean.

2.6 CONTROL EXPERIMENT 1: GRADUAL VS. ABRUPT DISAPPEARANCE OF THE FIXATION STIMULUS

The introduction of the moving rectangular plates produced a slight difference in the way the fixation stimulus disappeared between the gap and occlusion conditions: it disappeared all at once in the gap condition, but gradually in the occlusion condition. Thus, even though the temporal interval from the offset of the fixation stimulus to the onset of the target stimulus was identical in these two conditions (i.e., 200 ms), the

fixation stimulus began to disappear 50 ms earlier in the occlusion condition. The present experiment examined whether this difference affected performance in both the saccadic and manual reaction tasks.

Methods

In this control experiment, the same participants from Experiments 1 and 2 participated in saccadic and manual reaction tasks, respectively. The same stimuli from Experiment 1 were manipulated in two ways: (1) the plate color was changed to the background color (as in Experiment 3); and (2) only the last plate was used so that the fixation stimulus did not appear to “blink” in the pseudo-occlusion condition. All other stimuli and procedures were identical to those described in Experiment 1.

Results and Discussion

The results of the saccadic task indicated that the sudden vs. gradual disappearance of the fixation stimulus yielded only negligible differences in SRTs (191 ms vs. 189 ms, respectively: $t(9) = 0.96$, $p = 0.36$). In addition, for the gap and pseudo-occlusion conditions, SRT was shorter than that for the overlap condition (247 ms: $t(9) = 8.88$, $p < 0.001$ and $t(9) = 7.60$, $p < 0.001$, respectively). The manual task also yielded only negligible differences in MRTs for the gap and pseudo-occlusion conditions (364 ms vs. 361 ms, respectively: $t(9) = 0.82$, $p = 0.43$). Both conditions yielded a shorter MRT than that of the overlap condition (409 ms: $t(9) = 6.45$, $p < 0.001$ and $t(9) = 11.92$, $p < 0.001$, respectively). Thus, the results of the control experiment rule out the possibility that the

sudden vs. gradual disappearance of the fixation stimulus affected the differences in reaction times observed between the gap and occlusion conditions of the previous experiments.

2.7 CONTROL EXPERIMENT 2: MODULATION OF THE GENERAL WARNING EFFECT DUE TO THE POSSIBLE REAPPEARANCE OF THE OCCLUDED FIXATION STIMULUS

The introduction of the moving rectangular plates might also produce a difference in the effect of the general warning signal accompanied with the disappearance of the fixation stimulus between the gap and occlusion conditions. In particular, while the disappearance of the fixation stimulus in the gap condition informs the subsequent target onset, that in the occlusion condition informs only the possibility of the subsequent target onset due to the expected reappearance of the occluded fixation stimulus. Thus, the possible difference in the general warning effect might cause the observed difference in SRT between the gap and occlusion conditions in Experiments 1 and 3. In this control experiment, a typical method for controlling the difference in the general warning effect between the gap-overlap paradigms (i.e., presentation of an extra warning tone) was taken to test this possibility.

Methods

Ten new paid volunteers (four men and six women, aged 19–23 years) participated in the experiment. All participants had normal or corrected-to-normal vision and normal oculomotor function. All participants gave written informed consent prior to participation. To minimize the possible difference in the general warning effect between the fixation conditions, an extra warning tone (100 Hz for 10 ms) was presented 200 ms prior to the target onset in the stimuli of Experiment 1. The rest of the stimuli and procedures were identical to those described in Experiment 1.

Results and Discussion

The results were consistent with those obtained in Experiment 1. The mean SRTs for the gap, occlusion, and overlap conditions were 172 ms, 185 ms, and 220 ms, respectively. A repeated measures ANOVA showed a significant main effect of fixation condition ($F(2,18) = 30.53, p < 0.001$). Post-hoc pairwise comparisons with a Bonferroni correction revealed that the SRTs were significantly different for all combinations ($p < 0.01$). An additional two-way mixed ANOVA with fixation condition and auditory warning condition (with vs. without tone) as factors (i.e., comparisons to the results of Experiment 1) showed a significant main effect of fixation condition ($F(2,36) = 76.53, p < 0.001$) and auditory warning condition ($F(1,18) = 14.40, p < 0.005$), as well as a significant interaction ($F(2,36) = 7.40, p < 0.005$). Further analyses revealed that the main effect of the auditory warning condition was significant for the all gap, occlusion, and overlap conditions ($p < 0.05$ for all conditions); that is, the

presentation of an extra warning tone facilitated the SRTs of the all fixation conditions. Therefore, these results, especially the preservation of the difference in SRT between the gap and occlusion conditions, suggest that the observed difference in SRT between the gap and occlusion conditions in Experiments 1 and 3 cannot be fully explained by a possible modulation of the general warning effect due to the reappearance of the occluded fixation stimulus.

2.8 CONTROL EXPERIMENT 3: SUBJECTIVE IMPRESSION OF MAINTENANCE AND REAPPEARANCE OF AN OCCLUDED FIXATION STIMULUS

My interpretation of the results of Study 1 is based on the assumption that the fixation stimulus in the occlusion condition of Experiments 1 and 2 induced a subjective experience of phenomenal maintenance behind the rectangular plates, as well as the expectation of a re-emergence of the fixation stimulus, whereas only the expectation of re-emergence was experienced in the pseudo-occlusion condition of Experiments 3 and 4. In order to confirm these observations, the subjective impression of the fixation stimulus was subsequently examined with regard to phenomenal maintenance and re-emergence.

Methods

Participants

Ten new paid volunteers (eight men and two women, aged 19–25 years) were recruited. All had normal or corrected-to-normal vision and gave written informed consent prior to participation.

Stimuli and procedure

The same stimuli as in Experiments 1 and 3 were used, except that a mask stimulus with random-noise patterns ($12.0^\circ \times 9.0^\circ$) was presented in the center of the screen, after onset of the gap period and with the variable inter-stimulus intervals (ISIs) of 50/200/500 ms. The target stimulus was not presented. After presentation of the mask stimulus, the participants were asked if they thought the fixation stimulus was still there, or if they thought it would re-emerge. The two experiments were conducted in separate sessions. The participants engaged in both experiments and responded either “yes” or “no” by pressing the appropriate response keys on the keyboard. The participants were instructed to answer the questions according to their subjective impression. The order of the questions was counterbalanced across participants. There were 120 trials in which four gap conditions (the gap and occlusion conditions from Experiment 1 and the gap and pseudo-occlusion conditions from Experiment 3) were intermixed and presented in a random order.

Results and Discussion

The results of the experiments are depicted in Figure 8. A two-way repeated measures ANOVA (four gap conditions \times three ISIs) on the fixation maintenance question revealed a significant main effect of fixation condition ($F(3,27) = 9.75, p < 0.001$) and ISI ($F(2,18) = 14.76, p < 0.001$). The interaction was also significant ($F(6,54) = 3.08, p < 0.05$). A planned pairwise comparison with a Bonferroni correction revealed that the “maintaining” response rate in the occlusion condition of Experiment 1 was higher than that of other conditions ($p < 0.05$). No significant differences were found between the other conditions.

Regarding the fixation reappearance question, significant main effects were found for fixation condition ($F(3,27) = 9.40, p < 0.001$) and ISI ($F(2,18) = 4.85, p < 0.05$). Multiple comparisons revealed that the “re-emerging” response rate was higher in the occlusion and pseudo-occlusion conditions than in the gap conditions ($p < 0.05$), but that the “re-emerging” rates for the occlusion and the pseudo-occlusion conditions were comparable. Thus, the occlusion condition in Experiments 1 and 2 induced the subjective impression of maintenance, as well as the subjective impression and/or expectation of reappearance, while the pseudo-occlusion condition in Experiments 3 and 4 induced only the subjective impression and/or expectation of reappearance.

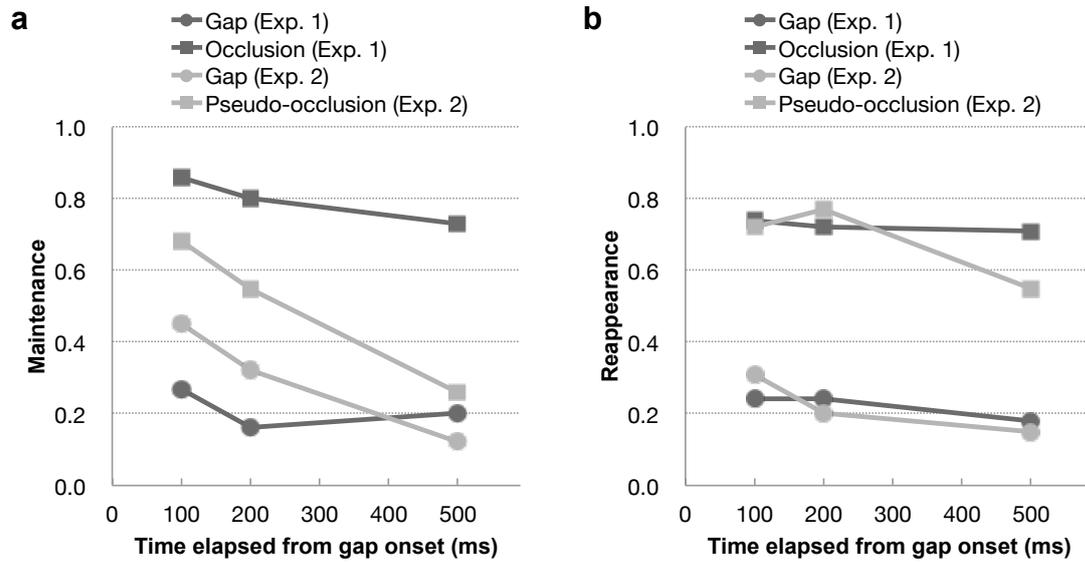


Figure 8. Mean evaluated subjective impressions of maintenance (a) and reappearance (b) of the fixation stimulus for each fixation condition. The horizontal axis represents the time elapsed from the gap onset, at which point participants were asked for their evaluations.

2.9 GENERAL DISCUSSION

The experiments of Study 1 examined the contributions of perceptual representation of a fixation stimulus on the saccadic and manual gap effects by manipulating phenomenal permanence of an occluded fixation point. The results of the saccadic reaction tasks (Experiment 1) demonstrated that response facilitation was maximized when the fixation stimulus disappeared both physically and subjectively (i.e., the gap condition). The magnitude of the facilitation was reduced when phenomenal permanence of the fixation stimulus existed, even when the retinal inputs of the fixation stimulus disappeared (i.e., the occlusion condition). Regarding the two putative components of subjective impression, the expectation of re-emergence of the fixation

stimulus rather than phenomenal permanence seemed to induce the delayed saccadic and manual responses. By contrast, in manual reaction tasks (Experiment 2), response facilitation occurred only when the fixation stimulus disappeared both physically and subjectively. The results of Control Experiments 1 and 2 confirmed that the observed difference in SRT between the gap and occlusion conditions in Experiments 1 and 3 was not due to the difference in the way the fixation stimulus disappeared (i.e., abrupt vs. gradual) nor due to the difference in the general warning effect. Thus, these results demonstrate that both physical and phenomenal components contribute to the saccadic gap effect, while the phenomenal component mainly determines the manual gap effect. The following sections discuss the results in terms of the current dominant theories of the gap effect: attentional predisengagement theory and the fixation offset effect.

The saccadic and manual gap effects are thought to have a close relation to attentional disengagement. Jin and Reeves (2009) demonstrated that attention was released more efficiently when the fixation stimulus disappeared compared to when the fixation stimulus remained or when it was replaced by another object. Pratt et al. (2006) found that removal of the attended portion of a stimulus produced a shorter saccadic latency compared to the removal of the unattended portion. The results of the present study demonstrate that the gap effect was hindered when the observers expected that the attended object would re-emerge after its physical disappearance. This finding is compatible with a recent neuroimaging study indicating that both inter- and intra-individual slower saccade reactions in the gap condition were positively correlated

with higher cortical control (Ozyurt and Greenlee, 2011). Moreover, no saccadic response facilitation has been observed in a blink gap condition in which the physical input of a fixation stimulus was removed during the same time period as the gap condition by a short airpuff (Rambold, El Baz, & Helmchen, 2004). These blink and occlusion gaps would induce a similar subjective impression that the physically disappeared fixation stimulus will reappear when the blink or occlusion period ends. Thus, in the present study, it is likely that attentional disengagement from the fixation stimulus was disrupted by the expectation of the re-emergence of the fixation stimulus even when it physically disappeared. This view is intuitively reasonable, as it seems beneficial to maintain attention to the location of an invisible object as long as the object is likely to re-emerge. Indeed, attention tends to be directed to and maintained on an object regardless of its visibility, rather than on retinal input *per se* (Churchland, Chou, & Lisberger, 2003; Flombaum, Scholl, & Pylyshyn, 2008; Joseph & Nakayama, 1999; Pratt & Sekuler, 2001; Zemel, Behrmann, Mozer, & Bavelier, 2002). Therefore, the gap effect does not completely correlate with the physical disappearance of retinal input, but also with allocation of attention caused by the expectation of the re-emergence of the fixation stimulus. This serves to postpone the subsequent response.

While subjective representation of the fixated stimulus almost entirely reduced the facilitation of manual responses, saccadic responses were still significantly faster in the occlusion and pseudo-occlusion conditions than in the overlap condition. One possible interpretation of this result is that, while the expectation of stimulus re-emergence

delays attentional disengagement, the oculomotor release or the fixation offset effect additively occurs as a result of the disappearance of physical inputs of the fixation stimulus. When a fixation stimulus is removed before a saccade, saccadic latency to a subsequent target tends to be shorter, regardless of whether the fixation stimulus was attended to (Kingstone & Klein, 1993; but see also Pratt et al., 2006). Neurophysiological studies have suggested that the fixation offset effect is mediated by subcortical, automatic mechanisms, particularly competition between inhibitory input from the fixation cells in the rostral pole of the SC and excitatory input from the movement cells in the intermediate layer of the SC (Dorris & Munoz, 1995; Munoz & Wurtz, 1992, 1993a). Furthermore, recent studies involving lesions of the SC have indicated that, in addition to saccadic execution, the SC plays important roles in relatively higher functions, such as target selection and selective attention (Goffart, Hafed, & Krauzlis, 2012; Lovejoy & Krauzlis, 2010; Song, Rafal, & McPeck, 2011). Therefore, it is plausible that the mechanism underlying oculomotor release functions in addition to that underlying higher-level factors such as attentional engagement played a role in the occlusion and pseudo-occlusion conditions of the present experiments.

Taken together, the experiments of Study 1 demonstrated that both retinal input and subjective expectation of the re-emergence of the fixation stimulus influence the saccadic gap effect, whereas the subjective representation of the fixation stimulus overcomes the effect of the physical disappearance of its retinal input for the manual gap effect. Thus, the physical disappearance of the fixation stimulus is not sufficient

and the subjective disappearance is necessary for inducing the saccadic and manual gap effects. Study 2 further investigated the necessity of the physical disappearance of the fixation stimulus in the saccadic and manual gap effects.

CHAPTER

3

Effects of the Subjective Disappearance and Physical Maintenance of a Fixation Stimulus on the Saccadic and Manual Gap Effects

3.1 INTRODUCTION

Study 1 (Chapter 2) examined the effects of the physical disappearance and subjective maintenance of a fixation stimulus on the saccadic and manual gap effects. The results of Study 1 demonstrated that the disappearance of physical inputs is not a sufficient condition for the saccadic gap effect, and that the subjective disappearance is also required. By contrast, the results of the manual reaction tasks demonstrated that the subjective disappearance of a fixation stimulus is necessary to induce the manual gap effect. By examining the effects of subjective disappearance and physical maintenance of a fixation stimulus on the saccadic and manual gap effects, Study 2 assessed whether

the physical disappearance of the fixation stimulus is necessary to induce the saccadic and manual gap effects.

To dissociate the physical disappearance and maintenance of a fixation stimulus from its subjective disappearance and maintenance, the present study investigated influences of an “invisible” fixation stimulus on the saccadic (Experiment 5) and the manual (Experiment 6) gap effects. Visibility of the disappearance and maintenance of the fixation stimulus was manipulated by using binocular rivalry (for reviews, see Blake & Logothetis, 2002; Lin & He, 2009) and the continuous flash suppression (CFS) technique (Tsuchiya & Koch, 2005). Binocular rivalry is a phenomenon of visual perception in which presentation of dissimilar visual stimuli to each eye causes observers to perceive random alternation of the two images, instead of a single, mixed image (see Figure 9a). The CFS technique is used to control the random alternation of perception in binocular rivalry, in which presenting a series of rapidly changing dynamic stimuli to one eye (i.e., the dominant eye) renders the supraliminal static stimuli to the other eye (i.e., the suppressed eye) invisible (see Figure 9b). Since the CFS can suppress supraliminal stimuli for a relatively long time (up to several minutes), it is a useful method for investigating the mechanisms underlying unconscious visual processing. Thus, the present study manipulated the disappearance and maintenance of the invisible fixation stimulus in the suppressed eye independently from the disappearance and maintenance of the visible fixation stimulus in the dominant eye. In order to confirm that the participants were not able to detect the suppressed fixation

stimulus at rates better chance, a screening experiment was performed before the main experiment (see Control Experiment 4 [Section 3.4] for details).

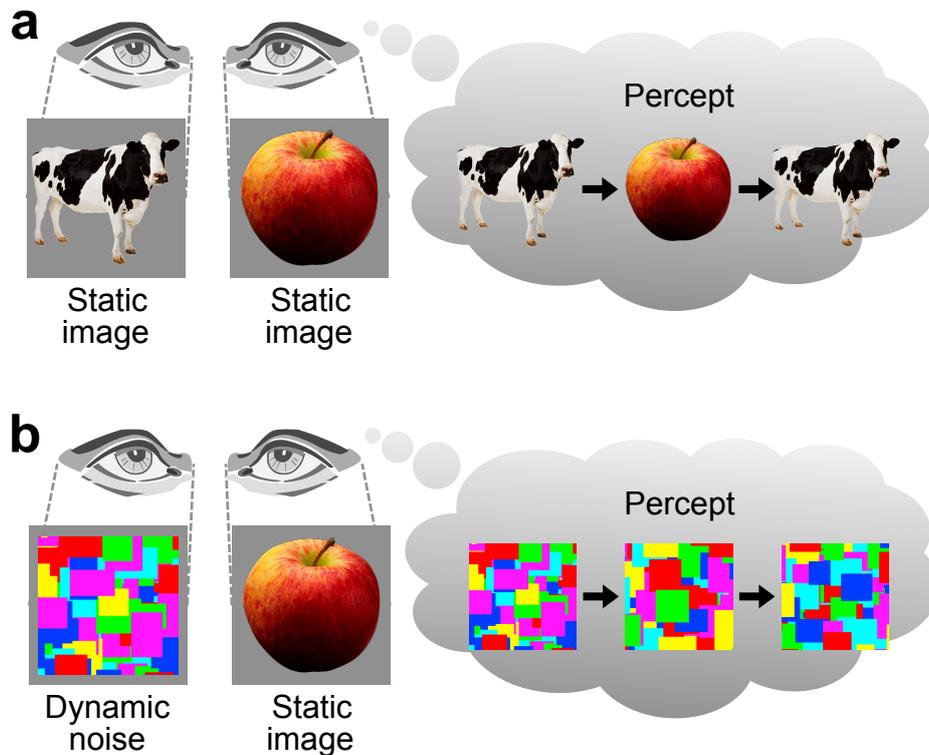


Figure 9. Binocular rivalry (a) and CFS (b). (a) Binocular rivalry is a phenomenon of visual perception in which presentation of dissimilar visual stimuli to each eye causes the perception of a randomly alternating image of the two stimuli instead of a single stable mixture of the two stimuli. (b) CFS is used to control the random alternation of perceiving stimuli in binocular rivalry in which presentation of a series of rapidly changing dynamic stimuli to one eye (i.e., dominant eye) renders the supraliminal static stimuli of the other eye (i.e., suppressed eye) invisible.

Previous studies on the gap effect have focused on how the consciously visible changes of a fixation point affect subsequent reactions; i.e., situations in which the observers were explicitly aware of the disappearance and maintenance of a fixation stimulus. However, the potential contributions of unconscious processes to the gap effect have been less studied. Invisible visual inputs may elicit visual processes to some

extent and affect visual perception as well as behavior (Almeida, Mahon, Nakayama, & Caramazza, 2008; Fang & He, 2005; Tamietto & de Gelder, 2010). For example, invisible stimuli are known to elicit various priming effects (i.e., enhancement, disruption, and alternation of subsequently processed stimuli) such as motion priming (Blake, Ahlstrom, & Alais, 1999), numerical (both symbolic and non-symbolic) priming (Bahrami et al., 2010), and pictorial object priming (Almeida et al., 2008; Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2012). Therefore, it is possible that the disappearance and maintenance of a fixation stimulus influences the gap effect even when it does not reach the level of awareness. In particular, oculomotor-specific processes might be modulated by the status of an invisible stimulus. In other words, the disappearance of an invisible fixation stimulus might cause partial oculomotor release and hence reduces saccadic latencies, or the maintenance of an invisible fixation stimulus might inhibit the oculomotor release and results in longer saccadic latencies.

In addition to saccade trials, key-press (i.e., manual) trials were also conducted to examine the contributions of conscious and unconscious processes on the manual gap effect. One question of interest is whether the facilitation of manual and saccadic responses arises from (or shares) the same mechanisms. Thus, another interest of Study 2 is to reveal whether the saccadic and manual gap effect share the same subcortical mechanisms by looking at the effect of the changes that occurs on the perceptually indivisible invisible fixation stimulus. Given that the saccadic gap effect primarily depends on the subcortical oculomotor system (i.e., the fixation offset effect) while the

manual gap effect depends more on cortical mechanisms, different effects of the invisible fixation stimulus are expected. More specifically, an invisible fixation stimulus should not affect decisional processes based on conscious awareness. Thus, the condition of the invisible fixation should only affect oculomotor-specific processes in the saccadic gap effect.

3.2 EXPERIMENT 5: EFFECTS OF THE DISAPPEARANCE AND MAINTENANCE OF AN INVISIBLE FIXATION STIMULUS ON THE SACCADIC GAP EFFECT

Experiment 5 examined the influence of an invisible fixation stimulus on the saccadic gap effect.

Methods

Participants

Thirteen new paid volunteers (seven men and six women, aged 19–26 years) participated in the experiment. All participants had normal or corrected-to-normal vision and normal oculomotor function. Twelve were able to reliably induce binocular suppression in the current experimental setting based on our criterion (see Control Experiment 4 [Section 3.4] for details) and therefore proceeded to the main experiment. All participants gave written informed consent prior to participation.

Experimental setup and apparatus

The experiment took place in a dark room. Participants were seated in front of a 21-inch CRT monitor (100 Hz) with their head stabilized on a chinrest at a viewing distance of 57 cm. Visual stimuli were viewed through handcrafted anaglyph glasses with Kodak gelatin filters of red (No. 25) and green (No. 58) for dichoptic presentation of the stimuli. The visual stimuli were generated with MATLAB (MathWorks) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). A desktop-mounted EyeLink 1000 (SR Research) controlled by the EyeLink Toolbox (Cornelissen et al., 2002) for MATLAB was used to record eye movement.

Stimuli

The visual stimuli (see Figure 10) were a fixation and a target dot (0.4° in diameter). The fixation dot was presented on the center of the screen and the target dot was presented 4.0° to the left or right of the fixation dot. Mondrian-like patterns ($3.0^\circ \times 3.0^\circ$), which changed at 10 Hz, were presented on the center of the screen to induce CFS. All the stimuli were presented within a rectangular frame ($12.0^\circ \times 6.0^\circ$).

Procedure

Each trial began with the presentation of the fixation stimulus and CFS stimuli for 1000 to 2000 ms (see Figure 10). The fixation stimulus was presented to both eyes while the CFS stimuli were presented to the pre-selected dominant eye. Participants were instructed to keep their eyes on the fixation point until the target appeared. After

the fixation period, the fixation stimulus was removed either from both eyes (binocular-gap condition), from the dominant eye only (dominant-eye-gap condition), or from the suppressed eye only (suppressed-eye-gap condition), or remained on in both eyes (binocular-overlap condition). After 200 ms, the target stimulus appeared to the left or right of the fixation location. Participants were instructed to make a saccade toward the target as quickly and accurately as possible. The target remained for 1000 ms. Trials were separated by a 1000-ms inter-trial interval that was indicated by a tone.

The experiment was a 2×2 within-subject design with visible fixation condition (gap or overlap) and invisible fixation condition (gap or overlap) as factors. The visible fixation to the dominant eye disappeared in the binocular-gap and dominant-eye-gap conditions whereas it remained in the suppressed-eye-gap and binocular-overlap conditions. By contrast, the invisible fixation to the suppressed eye disappeared in the binocular-gap and suppressed-eye-gap condition whereas it remained in the dominant-eye-gap and binocular-overlap conditions.

The experiment consisted of 160 trials in which the four gap conditions (40 trials each) were intermixed and presented in a random order. Before the experiment, the eye tracker was calibrated using nine reference points. Drift correction was also performed every 40 trials.

Data acquisition

Eye movements were recorded at a sampling rate of 500 Hz. The saccadic reaction time (SRT) was defined as the time from the target onset to a saccade onset. Saccade onset was detected as the time at which the eye movement velocity exceeded a threshold of $30^\circ/s$. As in Study 1, trials with SRTs of less than 110 ms (considered anticipatory responses) or greater than 534 ms (indicating lack of participant alertness) were excluded from data analysis (see Methods of Experiment 1 [Section 2.2] for a detailed description of the cut-off criteria). Responses were considered incorrect if the first saccade after target presentation was not directed toward the target; these trials were also excluded from the analysis. Application of these criteria resulted in the removal of 3% of trials from the analysis.

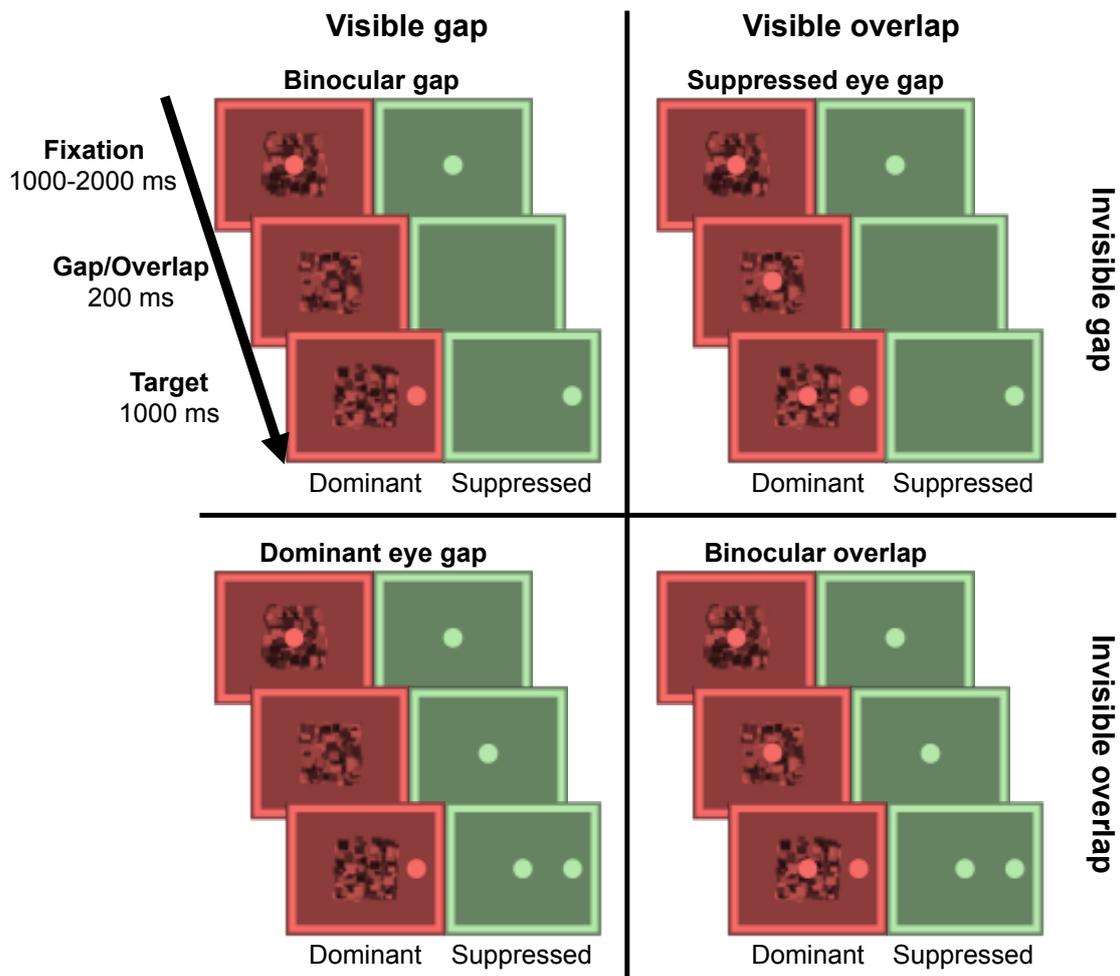


Figure 10. Schematic illustration of the trial sequences in Experiment 5. Each trial started with the presentation of a fixation stimulus in both eyes and a CFS stimulus only in the dominant eye. Then, the fixation stimulus was removed from both eyes (binocular-gap), only from the dominant eye (dominant-eye-gap), or only from the suppressed eye (suppressed-eye-gap), or remained in both eyes (binocular-overlap). After a 200-ms delay period, a target stimulus was presented at the left or the right of the fixation position in both eyes.

Results and Discussion

The results of Experiment 5 are shown in Figure 11. The mean SRTs for the binocular-gap, dominant-eye-gap, suppressed-eye-gap, and binocular-overlap conditions were 208 ms, 216 ms, 269 ms, and 266 ms, respectively. A two-way

repeated-measures ANOVA with visible fixation (gap vs. overlap) and invisible fixation (gap vs. overlap) conditions as factors showed a significant main effect of visible fixation condition ($F(1,11) = 87.20, p < 0.001$), but no effect of invisible fixation condition ($F(1,11) = 0.81, p = 0.39$). The interaction was also significant ($F(1,11) = 6.48, p < 0.05$). Further analyses revealed that the simple main effect of the visible fixation condition was significant regardless of the invisible condition (gap: $F(1,22) = 92.75, p < 0.001$; overlap: $F(1,22) = 60.98, p < 0.001$), whereas that of the invisible condition was significant in the visible gap condition ($F(1,22) = 5.70, p < 0.05$), but not in the visible overlap conditions ($F(1,22) = 1.14, p = 0.30$).

The results of the present experiment indicate that the magnitude of the saccadic gap effect was predominantly determined by the visible fixation condition. This is not surprising because the disappearance of a visible fixation stimulus induced the general warning effect, oculomotor-release (at least monocular), and/or attentional disengagement. However, the effect of invisible fixation on the visible gap conditions suggests that the maintenance of an invisible fixation stimulus interfered with response facilitation by the offset of a visible fixation. Alternatively, the absence of an effect in the invisible fixation condition on the visible overlap conditions suggests that the disappearance of an invisible fixation stimulus did not cause response facilitation when observers were unaware of the change. This result also implies that the disappearance of an invisible fixation alone cannot induce the general warning effect.

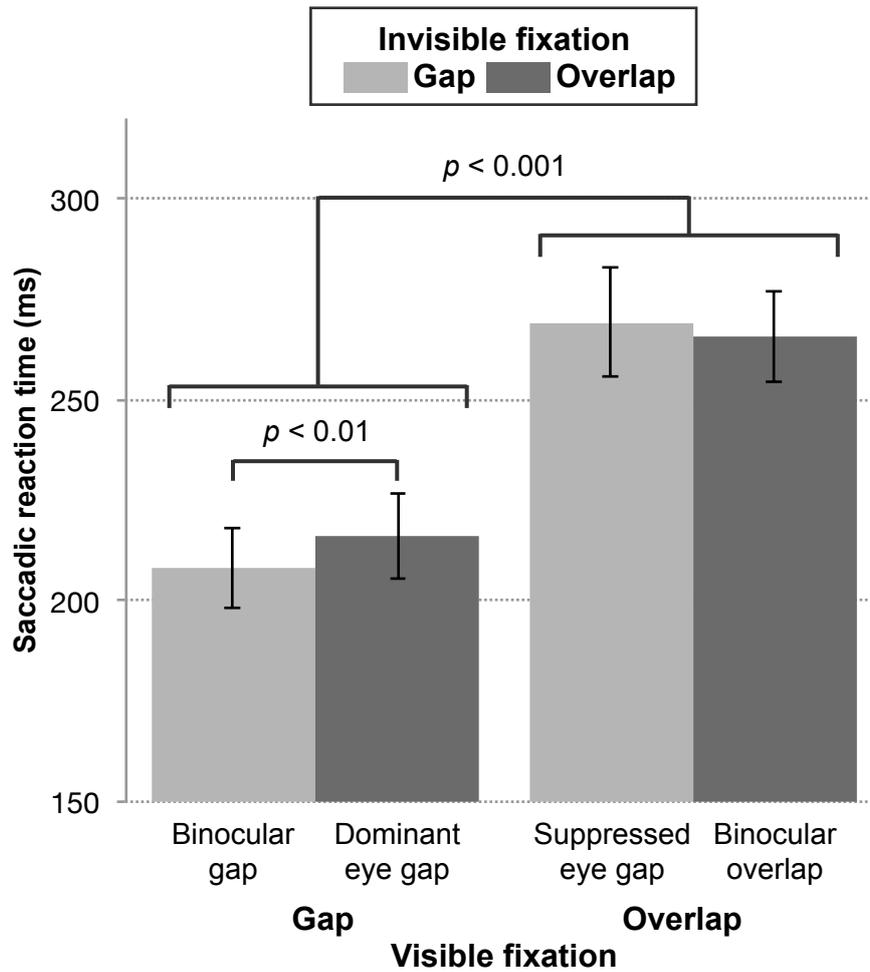


Figure 11. Mean SRTs in Experiment 5. Error bars represent the between-subject standard error of the mean.

3.3 EXPERIMENT 6: EFFECTS OF DISAPPEARANCE AND MAINTENANCE OF AN INVISIBLE FIXATION STIMULUS ON THE MANUAL GAP EFFECT

Experiment 6 examined the influence of an invisible fixation stimulus on the manual gap effect.

Methods

Thirteen new paid volunteers (ten men and three women, aged 19–24 years) participated in the experiment. All had normal or corrected-to-normal vision and normal eye-hand coordination function. One participant who did not meet the criterion for reliable binocular suppression in the screening test (see Control Experiment 4 [Section 3.4] for details) was excluded from the main experiment. All provided their written informed consent prior to participation.

The stimuli and procedures were identical to Experiment 5, except that the participants were instructed to respond to the target by pressing one of the corresponding left or right arrow keys on the keyboard as quickly and accurately as possible.

The manual reaction time (MRT) was defined as the time from the target onset to the key press. Trials with MRTs less than 210 ms or greater than 624 ms and those with incorrect responses were excluded from data analysis (see Methods of Experiment 1 [Section 2.2] for a detailed description of the cut-off criteria). These criteria resulted in the removal of 3% of trials from the analysis.

Results and Discussion

Figure 12 depicts the results of Experiment 6. The mean MRTs for the binocular-gap, dominant-eye-gap, suppressed-eye-gap, and binocular-overlap conditions were 351 ms, 345 ms, 374 ms, and 375 ms, respectively. A two-way

repeated-measures ANOVA with visible fixation and invisible fixation conditions as factors showed a significant main effect of the visible fixation condition ($F(1,11) = 28.51, p < 0.001$). However, neither the main effect of the invisible fixation condition ($F(1,11) = 1.06, p = 0.33$) nor the interaction ($F(1,11) = 0.97, p = 0.35$) was significant.

The results of Experiment 6 indicate that, unlike for the saccadic gap effect, only visible information influences the manual gap effect. Although the results of Experiment 6 alone do not specify the primary component of the manual gap effect, the difference in the influence of the invisible fixation stimulus suggests that the mechanisms underlying the manual and saccadic gap effects are partially different.

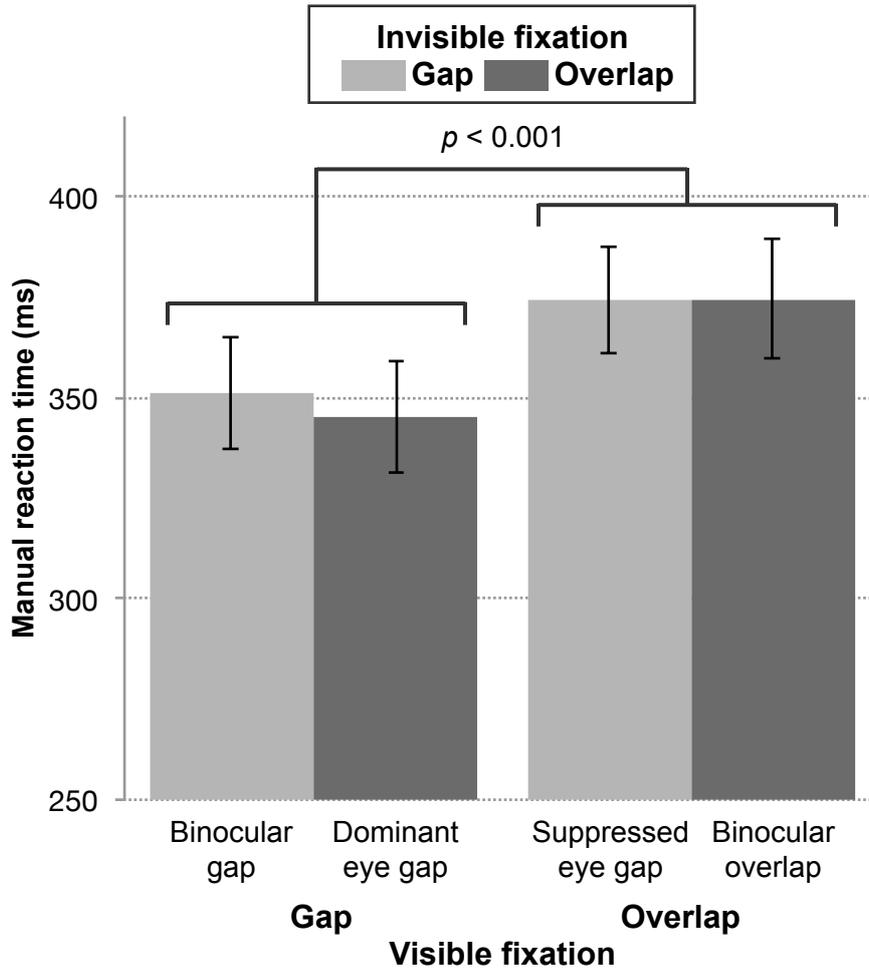


Figure 12. Mean MRTs in Experiment 6. Error bars represent the between-subject standard error of the mean.

3.4 CONTROL EXPERIMENT 4: OBJECTIVE MEASURES OF THE SUPPRESSION EFFECTIVENESS

All the participants took part in a screening experiment prior to the main experiment in order to confirm that the CFS successfully resulted in an invisible fixation stimulus. A two interval-forced choice detection task was conducted with a pair of fixation stimuli presented with a 1000-ms inter-stimulus interval. The fixation

stimulus was identical to that in the main experiment. Participants were asked to choose an interval in which the fixation stimulus remained until the completion of stimulus presentation. A tone announced the end of stimulus presentation for each interval. The stimulus pairs consisted of the fixation stimulus from the binocular-gap and the dominant-eye-gap conditions (64 test trials). In addition, 16 catch trials were presented; in these, the stimuli were the fixation stimuli from the binocular-gap and binocular-overlap conditions. Thus, each participant performed 80 trials in which the test and catch trials were intermixed and presented in random order. Three participants who showed a significantly higher detection rate than chance (a one-tailed binomial test against 0.5, $p < 0.05$) were excluded from the main experiment. The screening experiment, therefore, assured that the visual input (i.e., the fixation stimulus) to the suppressed eye was rendered invisible by the CFS; the mean detection rates were 0.5126 (SD = 0.0473) and 0.9796 (SD = 0.0366) for the test and catch trials, respectively.

3.5 GENERAL DISCUSSION

The objective of Study 2 was to highlight the contribution of unconsciously processed information on the gap effect. The effects of the disappearance and maintenance of an invisible fixation stimulus on the saccadic gap effect (Experiment 5) and the manual gap effect (Experiment 6) were examined. The results showed that the disappearance of a visible fixation stimulus caused a robust response facilitation in both

saccadic and manual tasks, regardless of the disappearance or maintenance of the invisible fixation. In contrast, the effect of the invisible fixation stimulus differed between the saccadic and manual gap effects. In particular, the maintenance of the invisible fixation reduced the saccadic gap effect but had no effect on the manual gap effect. The implications of Study 2 are twofold: (1) the saccadic gap effect is partly mediated by unconscious processes; and (2) the processes underlying the saccadic and manual gap effects are partially separable.

The components of the gap effect, the general warning effect and the facilitation caused by the disappearance of the fixation point, have sometimes been confounded. Typically, the two processes have been dissociated by showing further response facilitation by the disappearance of the fixation stimulus when an extra warning stimulus (e.g., a tone) is presented (Pratt et al., 2000; Reuter-Lorenz et al., 1991). The comparable reaction times between the suppressed-eye-gap and binocular-overlap conditions in Experiments 5 and 6 indicate that the disappearance of an invisible fixation stimulus does not serve as a warning signal. Nevertheless, the greater response facilitation in the binocular-gap condition compared to the dominant-eye-gap condition in Experiment 5 indicates that the disappearance of an invisible fixation stimulus does affect the saccadic gap effect. Thus, the results of Study 2 provide further evidence that the processes specific to the disappearance of the fixation stimulus that are unrelated to the general warning effect do contribute to the saccadic gap effect.

In the saccadic gap effect, maintenance of the invisible fixation stimulus slightly but significantly reduced response facilitation when the visible fixation stimulus was removed. This result can be interpreted in two ways by current gap effect theories. First, according to the fixation offset effect, the longer saccadic latency caused by the maintenance of the invisible fixation stimulus might be due to failure or disruption of a proper oculomotor release from automatic fixation processes. The fixation offset effect assumes that the saccadic gap effect occurs because the disappearance of the fixation stimulus leads to the release of the active fixation state and allows efficient initiation of saccades to a new location (Fendrich et al., 1991; Kingstone & Klein, 1993; Munoz & Wurtz, 1992). This view is supported by neurophysiological studies in non-human primates that have shown that a fixation state is associated with the activation of fixation-related neurons in the rostral pole of the SC, and that those activations inhibit the activation of saccade-generating neurons in the intermediate layer of the SC (Dorris & Munoz, 1995; Munoz & Wurtz, 1992, 1993a, 1993b). Unlike subliminal stimuli whose intensity is too weak to consciously perceive or stimuli in the visual masking technique whose presentation time is too short to consciously perceive, the suppressed fixation stimuli in Study 2 had physical inputs that allow awareness of the stimuli under conditions of no suppression (for reviews, see Blake & Logothetis, 2002; Lin & He, 2009; Pessoa, 2005). Thus, it is plausible that the physical inputs from the invisible fixation stimulus interfered with the oculomotor release from the fixation location prior to the target onset, and that this process was governed by subcortical mechanisms (i.e., the fixation offset effect).

Another possible interpretation of the results of Study 2 is that disengagement of attention, which supposedly occurs before target onset at the point of disappearance of the fixation stimulus, failed due to the maintenance of the invisible fixation stimulus. The attentional predisengagement theory assumes that the gap effect occurs because the disappearance of a fixation stimulus accompanies the disengagement of attention from the fixation. In other words, the maintenance of a fixation stimulus (i.e., the overlap condition) requires additional attentional disengagement processes after target onset in order to initiate the next saccadic or manual response. In short, in the present experimental setting, this assumption was true if attention was engaged by the invisible fixation stimulus. Invisible stimuli, especially of emotionally arousing stimuli, are known to capture spatial attention (Jiang, Costello, Fang, Huang, & He, 2006). Furthermore, several studies has also demonstrated that suppressed invisible stimuli are processed to some extent, especially via the dorsal pathway (Almeida et al., 2008; Fang & He, 2005; Roseboom & Arnold, 2011; Sakuraba et al., 2012; Spering, Pomplun, & Carrasco, 2011). Therefore, although the fixation stimulus in the present study was emotionally neutral, the possibility that the maintenance of the invisible fixation stimulus interfered with disengagement of attention cannot be ruled out.

Unlike for the saccadic gap effect, only the visible fixation stimulus was relevant to the manual gap effect. That is, no effect of the invisible fixation stimulus was found. Previous studies have indicated that the disappearance of a fixation point does not facilitate manual responses when the temporal warning effect was controlled

(Reuter-Lorenz et al., 1991; Tam & Ono, 1994). Thus, several studies have suggested that the primary component of the manual gap effect is the general warning effect (Jin & Reeves, 2009; Kingstone & Klein, 1993; Reuter-Lorenz et al., 1991; Tam & Ono, 1994; but see also Pratt et al., 1999). Furthermore, the lack of interference in a dual task (making a saccade and manual movement in one task) indicates that the saccadic and manual gap effects might be mediated by two distinct mechanisms (Jin & Reeves, 2009). The present study adds further support to this hypothesis. If the primary component of the manual gap effect is the general warning effect, the MRTs in the current experiment should have only depended on the event occurring in the dominant eye because the warning signal was the offset of the visible fixation stimulus. This was demonstrated in the results of Experiment 5, in which the offset of the invisible fixation stimulus did not cause any response facilitation (i.e., no warning effect occurred). In other words, the present results indicate that the monocular disappearance of the fixation stimulus does not serve as a temporal cue or induce a general warning unless the observer is aware of it. Therefore, the fixation offset effect or attentional disengagement might not be involved in the manual gap effect.

In summary, the experiments of Study 2 demonstrated that while the disappearance of a visible fixation stimulus predominantly determined the magnitude of the saccadic gap effect, maximal response facilitation occurred only when the fixated stimulus disappeared both physically and subjectively. By contrast, the subjective disappearance of a fixation stimulus induced the manual gap effect regardless of the physical

maintenance of an invisible fixation stimulus. The results of the present experiments by themselves do not specify the primary components of the gap effects. However, these results do indicate that partially different processes mediate the saccadic and manual gap effects. Moreover, the dependence of unconscious information observed only in the saccadic gap effect is evidence for the oculomotor-specific component in the gap effect.

CHAPTER

4

Effects of Social Signals from a Gaze-Fixation Stimulus on the Saccadic and Manual Gap Effects

4.1 INTRODUCTION

The Study 1 (Chapter 2) demonstrated that the expectation of the reappearance of an occluded fixation point (i.e., phenomenal permanence or a tunnel effect: Burke, 1952; Gibson et al., 1969; Michotte, 1950) inhibited the gap effect even when the fixation point physically disappeared (Ueda, Takahashi, & Watanabe, 2013). The results suggest that response facilitation in the gap effect can be influenced by a subjective interpretation of how the fixation stimulus is removed. In other words, higher perceptual components contribute to the gap effect. Study 3 (Chapter 4) further investigated whether a higher cognitive function, especially gaze perception, influences response facilitation in the gap effect.

As a social signal, direct gaze (i.e., eye contact) from others carries a wealth of social information. The physical difference in the visual images of a direct vs. an

averted gaze is subtle, but eye contact involving a direct gaze is known to have special social implications (for reviews, see Emery, 2000; Senju & Johnson, 2009). Several studies have reported that people are highly sensitive to direct gazes from others. For instance, in the visual search paradigm, detecting a direct gaze among averted-gaze distractors is easier than detecting an averted gaze among direct-gaze distractors (Conty et al., 2006; Doi & Ueda, 2007; Palanica & Itier, 2011; Senju et al., 2005; von Grünau & Anston, 1995). In addition, Senju and Hasegawa (2005) have demonstrated that direct gaze can capture spatial attention and interfere with attentional disengagement (i.e., breaking eye contact).

Study 3 investigated whether a visual stimulus containing social signals modulates response facilitation in the gap effect. More specifically, the effects of the presence vs. absence of eye contact from a fixated cartoon face on the gap effect were examined. Experiments 7 and 8 examined the effects of fixation-gaze direction changes shortly before target presentation on the saccadic and manual gap effects, respectively. In these experiments, the gaze direction changed from averted to direct (i.e., the appearance of eye contact) or from direct to averted (i.e., the disappearance of eye contact). By removing the facial features from the facial fixation, Experiments 9 and 10 further investigated the effects of the geometric properties of gaze shift on the saccadic and manual gap effects, respectively. Finally, Experiment 11 investigated the effects of abrupt presentation of direct or averted gazes, rather than a shift in gaze directions, on the subsequent saccadic responses.

4.2 EXPERIMENT 7: EFFECTS OF THE DISAPPEARANCE AND APPEARANCE OF EYE CONTACT ON SACCADIC RESPONSES

Experiment 7 examined the influence of the disappearance and appearance of eye contact from the fixation face before the target onset on the subsequent target-elicited saccadic responses.

Methods

Participants

Ten paid volunteers (two men and eight women, aged 20–33 years) participated in the experiment. All had normal or corrected-to-normal vision and normal oculomotor function. All participants gave written informed consent prior to participation.

Experimental setup and apparatus

The experiment took place in a dark room. Participants sat with their heads stabilized on a chinrest mounted at a viewing distance of 57 cm. Visual stimuli were generated by MATLAB (MathWorks) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) and were presented on a 21-inch CRT monitor with a 100 Hz refresh rate. Eye movements were recorded with the EyeLink 1000 eye tracker system (SR Research) at a sampling of 250 Hz, using the MATLAB EyeLink Toolbox extensions (Cornelissen et al., 2002).

Stimuli

A cartoon face (see Figure 13) consisted of a round gray face surface ($2.5^\circ \times 2.5^\circ$, 10.3 cd/m^2), a lined nose and mouth (1.2 cd/m^2), scleras (i.e., the whites of the eyes: 0.7° , 64.2 cd/m^2) and pupils (0.2° , 1.2 cd/m^2). The cartoon was presented on the center of the screen. The pupils of the eyes were placed either at the center or 0.2° above/below the center of the scleras for the direct and averted gazes, respectively. A white target dot (0.4° in diameter, 37.9 cd/m^2) was presented 8.0° to the left or right of the center of the face. All 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 1000–2000 ms (see Figure 13). The participants were instructed to fixate on the eyes of the face, but they were not told to fixate on a particular (left or right) eye. Then, the pupils were removed from the eyes (the gap condition), remained unchanged (the overlap condition), or were displaced vertically (the vertical shift condition). After a 200-ms delay, a target appeared to the left or right of the fixation stimulus. The participants were asked to make a saccade toward the target as quickly as possible. Trials were separated by a 1000-ms inter-trial interval that was signaled by a tone.

The experiment was a 2×3 within-subjects design with initial gaze direction (direct or averted) and fixation condition (gap, vertical shift, or overlap) as factors. Of particular interest was the effect of the vertical shift condition, in which gaze was initially direct and changed to averted, or was initially averted and 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), while the latter 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 eye tracker was calibrated for each observer using nine reference points. Drift correction of the eye tracker was also conducted every 48 trials. Observers were allowed to take a short break prior to the drift correction, if they requested.

Data acquisition

Eye movements were recorded at a sampling rate of 500 Hz. The saccadic reaction time (SRT) was defined as the time from the target onset to a saccade onset, and the saccade onset was defined as the time at which the eye movement velocity exceeded a threshold of $30^\circ/\text{s}$.

Trials with SRTs of less than 90 ms or of greater than 470 ms were excluded from further analyses (see Methods of Experiment 1 [Section 2.2] for a detailed description of the cut-off criteria). Trials in which the first saccade after the target onset were

directed toward an incorrect target side were also excluded. These criteria resulted in the removal of 2% of the trials from the analysis.

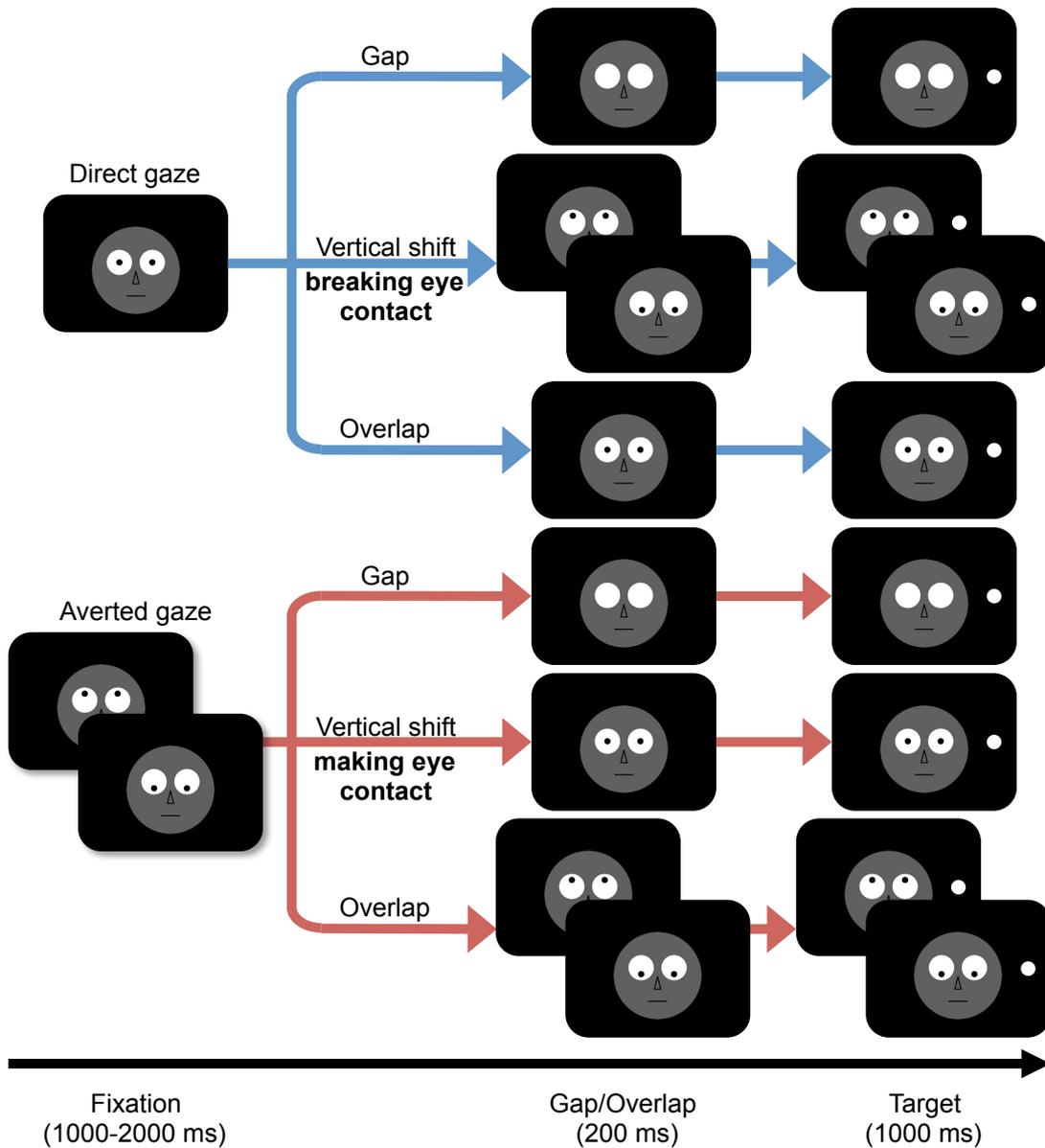


Figure 13. Schematic illustration of the trial sequences in Experiment 7. Each trial started with the presentation of a cartoon face with direct or averted gaze that served as a fixation stimulus. Then, the pupils of the face disappeared (gap), shifted vertically (vertical shift), or remained (overlap). After a 200-ms delay period, a target dot appeared at the left or right of the fixation face.

Results and Discussion

The results of Experiment 7 are shown in Figure 14 and Table 1. A two-way repeated-measures ANOVA with initial gaze direction (direct vs. averted) and fixation condition (gap vs. vertical shift vs. overlap) as factors showed significant main effects of initial gaze direction ($F(1,9) = 11.32, p < 0.01$) and fixation condition ($F(2,18) = 11.17, p < 0.001$), as well as a significant interaction ($F(2,18) = 5.95, p < 0.05$). Further analyses revealed that the main effect of initial gaze direction was significant only in the vertical shift condition ($F(1,27) = 23.16, p < 0.001$), but neither the gap ($F(1,27) = 1.73, p = 0.20$) nor the overlap condition ($F(1,27) = 1.67, p = 0.21$). By contrast, the main effect of fixation condition was significant for both the direct initial gaze ($F(2,36) = 8.83, p < 0.001$) and the averted initial gaze ($F(2,36) = 11.83, p < 0.001$); however, this effect was somewhat different depending on the initial gaze direction. When the initial gaze was direct, the SRT of the vertical shift condition was relatively comparable to that of the gap condition ($p = 0.07$), whereas it was shorter than that of the overlap condition ($p < 0.05$). Conversely, when the initial gaze was averted, the SRT of the vertical shift condition was significantly longer than that of the gap condition ($p < 0.001$), but was comparable to that of the overlap condition ($p = 0.94$). In other words, the change from a direct to an averted gaze (i.e., disappearance of eye contact) shortened saccadic latency in a manner similar to the physical removal of the fixation stimulus, whereas the change from an averted to a direct gaze (i.e., the appearance of eye contact) did not shorten the saccadic latency as compared to conditions in which the fixation stimulus

was unchanged. These results suggest that the change from an averted to a direct gaze has a strong inhibitory effect that can cancel the general warning effect induced by a temporal cue (i.e., shift of the pupils). These results will be further discussed in the general discussion section.

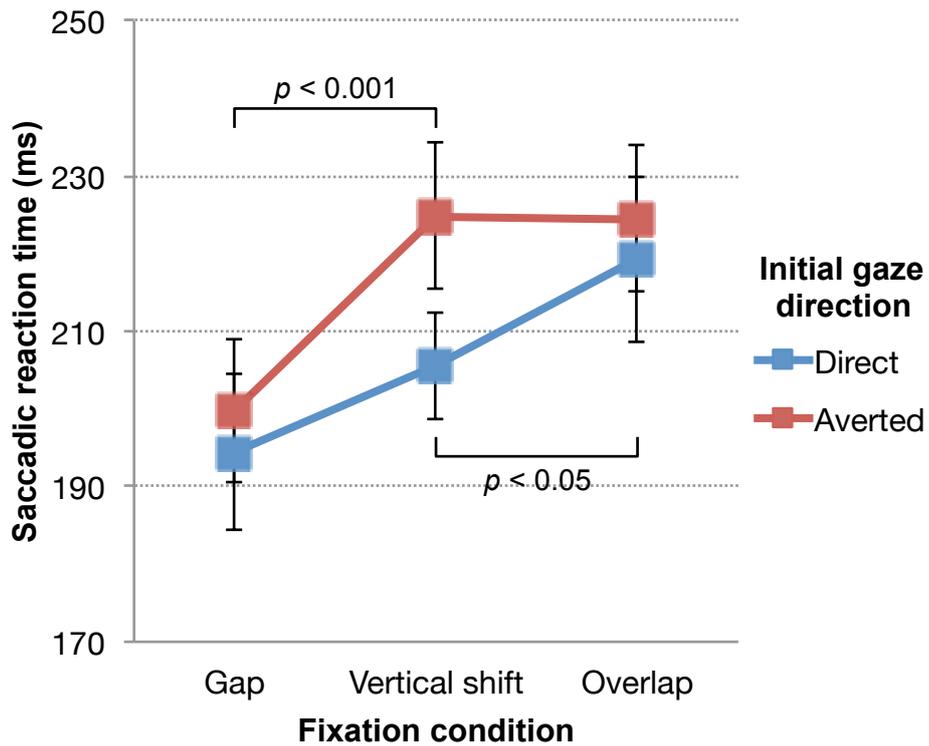


Figure 14. Mean SRTs in Experiment 7. Error bars represent the between-subject standard error of the mean.

Table 1. Mean SRTs (ms) in Experiment 7

Initial gaze direction	Fixation condition		
	Gap	Vertical shift	Overlap
Direct	194	205	219
Averted	200	225	224

4.3 EXPERIMENT 8: EFFECTS OF THE DISAPPEARANCE AND APPEARANCE OF EYE CONTACT ON MANUAL RESPONSES

Experiment 8 examined the influence of the disappearance and appearance of eye contact from the fixation face before target onset on the subsequent target-elicited manual responses.

Methods

Ten new paid volunteers (six men and four women, aged 18–25 years) participated in the experiment. All had normal or corrected-to-normal vision and normal eye-hand coordination. They gave written informed consent prior to participation.

The stimuli and procedures were identical to those used in Experiment 7, except that the participants responded to the target by pressing the corresponding left or right arrow key on the keyboard.

The manual reaction time (MRT) was defined as the time between the target presentation and either a left or a right key press. As in previous experiments, trials with incorrect responses and MRTs less than 200 ms or longer than 616 ms were removed from the analysis (see Methods of Experiment 1 [Section 2.2] for a detailed description of the cut-off criteria). These criteria resulted in the removal of 3% of the trials.

Results and Discussion

The results of Experiment 8 are shown in Figure 15 and Table 2. A two-way repeated-measures ANOVA with initial gaze direction and fixation condition as factors revealed a significant main effect of fixation condition ($F(2,18) = 10.64, p < 0.001$). However, unlike for the saccadic responses in Experiment 7, neither the main effect of initial fixation position ($F(1,9) = 0.48, p = 0.51$) nor the interaction was significant ($F(2,18) = 0.81, p = 0.46$). Post-hoc pairwise comparisons on the fixation condition revealed that the MRT of the vertical shift condition was significantly slower than that of the gap condition ($p < 0.005$), but was comparable to that of the overlap condition ($p = 0.23$).

A notable difference between the manual reaction tasks (Experiment 8) and the saccadic reaction tasks (Experiment 7) was that the effects of the fixation condition did not differ depending on the initial gaze direction in the manual reaction tasks. In both the initial gaze direction conditions, the MRTs of the vertical shift conditions were significantly longer than those of the gap conditions, and were comparable to those of the overlap conditions. These results can be interpreted in two ways. First, regardless of its direction, gaze shift prior to the target presentation inhibits response facilitation induced by the displacement of the pupils. This explanation is partially true because the shift of the pupils was certainly a sufficient condition for inducing the general warning effect (i.e., the vertical shift was a temporal cue for the subsequent target presentation). Second, the physical displacement by itself did not induce response facilitation more

than the general warning effect. These two possibilities were tested in Experiment 10 below.

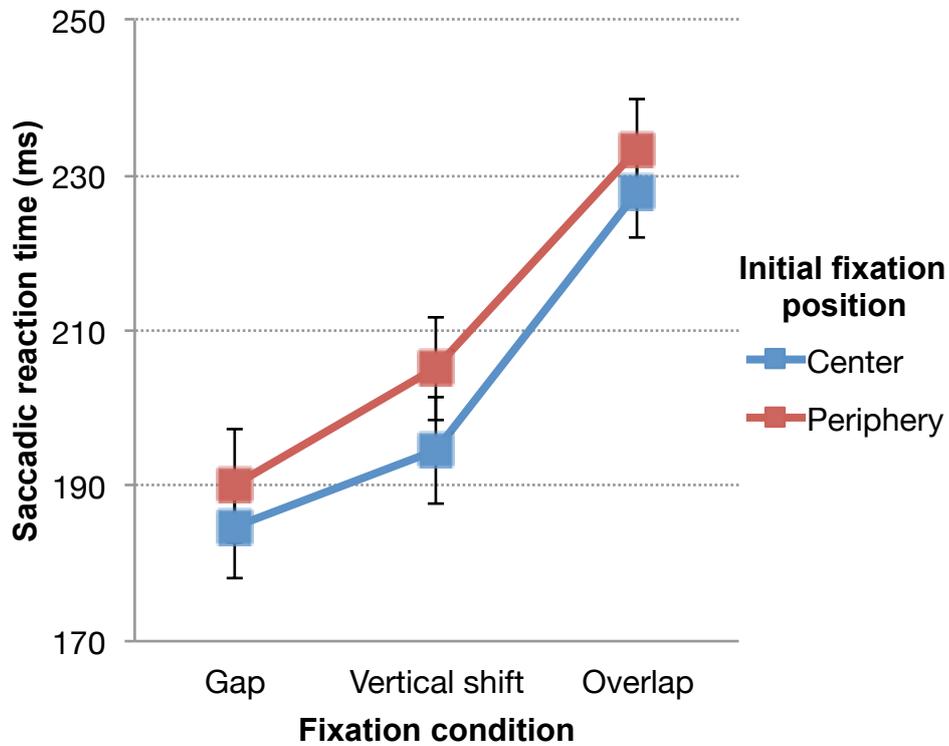


Figure 15. Mean MRTs in Experiment 8. Error bars represent the between-subject standard error of the mean.

Table 2. Mean MRTs (ms) in Experiment 8

Initial gaze direction	Fixation condition		
	Gap	Vertical shift	Overlap
Direct	323	243	346
Averted	326	341	350

4.4 EXPERIMENT 9: EFFECTS OF THE GEOMETRIC PROPERTY OF GAZE SHIFTS ON SACCADIC RESPONSES

The results of Experiment 7 implied that the disappearance or appearance of an eye contact signal from the fixation stimulus could modulate the gap effect. However, in the vertical shift conditions, although the distance of pupil displacement was the same between the direct-to-averted and averted-to-direct stimuli, the position of the pupil relative to the sclera was asymmetric. In the direct-to-averted shift, the pupils were shifted from the center to the periphery of the sclera, whereas in the averted-to-direct shift, they were shifted from the periphery to the center. Therefore, it is possible that these differences, rather than the social eye-contact signal, caused the observed differences in the gap effect. Furthermore, the results of Experiment 7 do not clearly indicate whether the direct-to-averted shift facilitated the saccade initiation or the averted-to-direct shift interfered with the saccade initiation. Therefore, the present experiment modified the fixation stimulus of Experiment 7 such that it could not provide a social impression. In particular, only a single pupil and sclera were used, and all other parts of the facial stimulus were removed (see Figure 16).

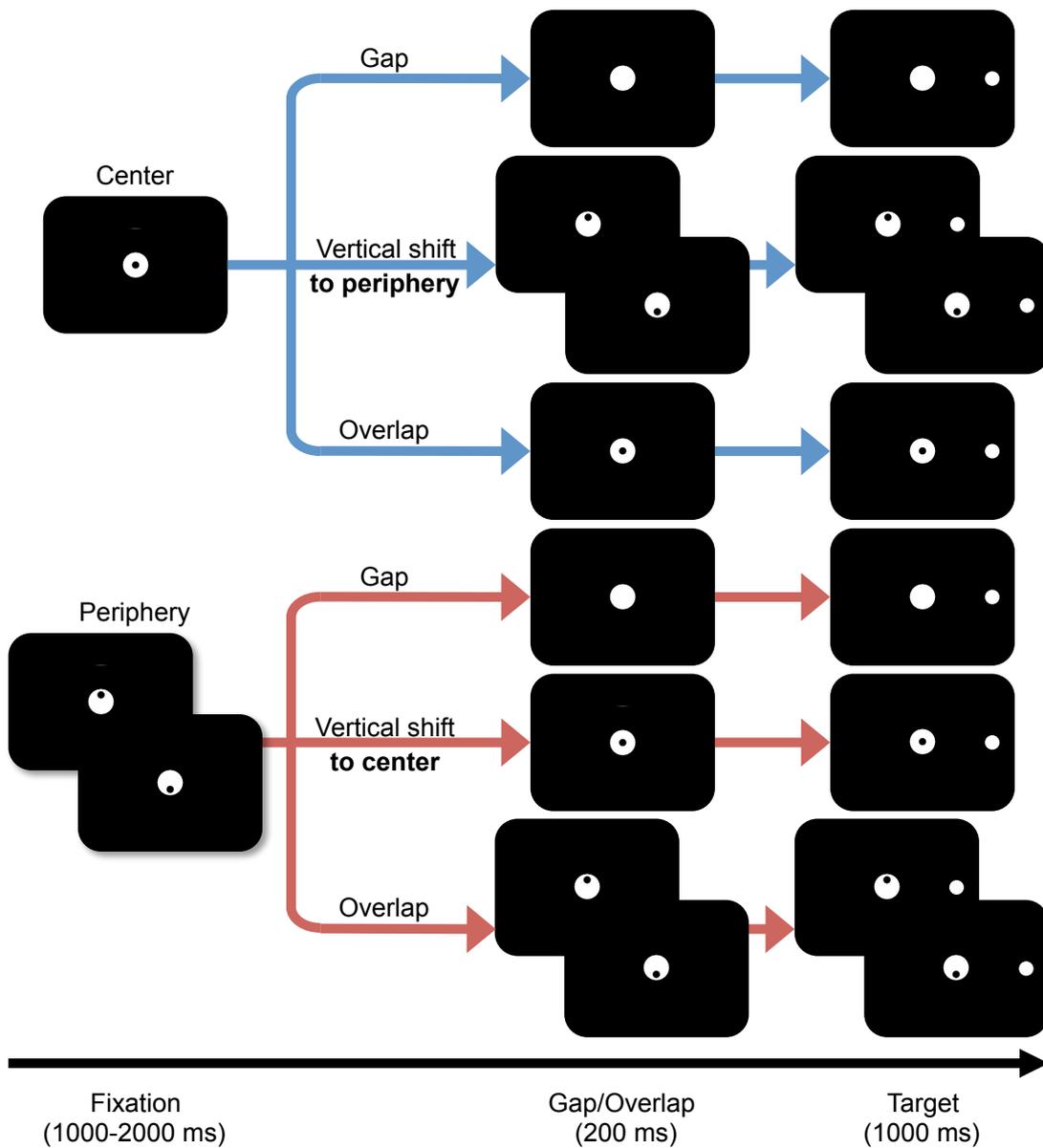


Figure 16. Schematic illustration of the trial sequences in Experiment 9. The pupil (black dot) and the sclera (white disk) of a single eye in Experiment 7 were used as experimental stimuli, where the observers were asked to fixate on the black dot within the white disk. All the other sequences were the same as in Experiment 7.

Methods

Ten paid volunteers (eight men and two women, aged 19–29 years) who had not participated in either Experiment 7 or 8 participated. All had normal or

corrected-to-normal vision and normal oculomotor function. All provided a written informed consent prior to participation.

The stimuli and procedures were identical to those used in Experiment 7, except that a single dot within a white disk (i.e., the pupil and the sclera of a single eye) was used as the fixation stimulus and was presented on the center of the screen. For confirmation, after the experiment, all the observers were asked if they perceived the fixation stimulus as an eye, and none reported doing so.

Results and Discussion

The results of Experiment 9 are shown in Figure 17 and Table 3. A two-way repeated-measures ANOVA with initial fixation position (center vs. periphery) and fixation condition (gap vs. vertical shift vs. overlap) as factors indicated a significant main effect of the initial fixation position ($F(1,9) = 7.65, p < 0.05$) and the fixation condition ($F(2,18) = 17.94, p < 0.001$). However, unlike the facial fixation stimulus in Experiment 7, no significant interaction was found between the initial fixation position and the fixation condition ($F(2,18) = 0.88, p = 0.43$). Post-hoc pairwise comparisons on the fixation condition revealed that the SRT of the vertical shift condition was comparable to that of the gap conditions ($p = 0.11$), but was significantly shorter than that of the overlap condition ($p < 0.001$).

No difference was found between the vertical shift conditions (center-to-periphery vs. periphery-to-center). These results imply that the modulation of the SRTs by the

gaze shifts in Experiment 7 was not due to a geometric property of the fixation stimulus, but was due to the disappearance and appearance of eye contact. Furthermore, the pattern of results observed in Experiment 9 was similar to that observed in the direct-to-averted shift condition (disappearance of eye contact) of Experiment 7. This implies that the effect of the social signal in the vertical shift condition of Experiment 7 was inhibition due to the appearance of eye contact, rather than facilitation due to the disappearance of eye contact. In other words, the disappearance of eye contact did not facilitate the saccadic initiation more than the physical displacement of the fixation stimulus did.

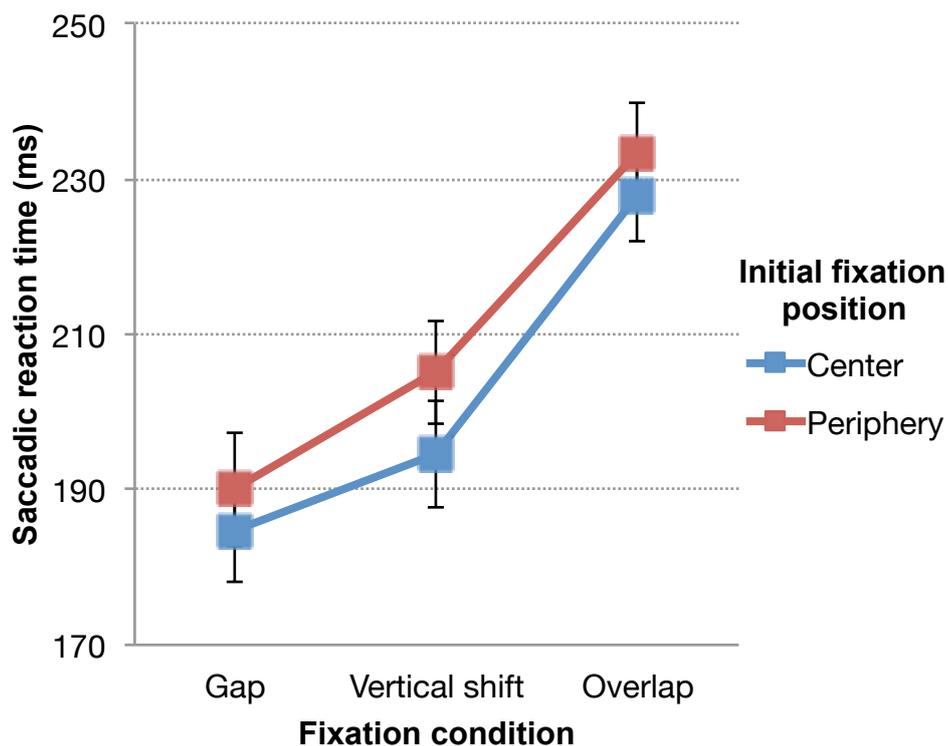


Figure 17. Mean SRTs in Experiment 9. Error bars represent the between-subject standard error of the mean.

Table 3. Mean SRTs (ms) in Experiment 9

Initial fixation position	Fixation condition		
	Gap	Vertical shift	Overlap
Center	185	195	228
Periphery	190	205	233

4.5 EXPERIMENT 10: EFFECTS OF THE GEOMETRIC PROPERTY OF GAZE SHIFTS ON MANUAL RESPONSES

Experiment 10 examined how the geometric properties of gaze shifts independent of the social signal affected the subsequent target-elicited manual responses.

Methods

Ten new paid observers (three men and seven women, aged 18–25 years) participated. All had normal or corrected-to-normal vision and normal eye-hand coordination. All gave written informed consent prior to participation.

The same experimental stimuli and procedures as in Experiment 9 were used, except that the participants were asked to respond to the target by pressing the corresponding left or right key on the computer keyboard. All the observers were asked if they perceived the fixation stimulus as an eye at the end of trials, and none reported doing so.

Results and Discussion

The results of Experiment 10 are shown in Figure 18 and Table 4. A two-way repeated-measures ANOVA with initial fixation position and fixation condition as factors showed a significant main effect of fixation condition was significant ($F(2,18) = 21.78, p < 0.001$). Neither the main effect of initial fixation position ($F(1,9) = 0.04, p = 0.85$) nor the interaction was significant ($F(2,18) = 0.12, p = 0.89$). Pairwise comparisons on the fixation condition revealed that, unlike the saccadic reactions in Experiment 9, the manual reactions in the vertical shift condition were significantly slower than were those in the gap condition ($p < 0.001$), but were relatively comparable to those in the overlap condition ($p = 0.06$). In other words, these results were identical to those of Experiment 8.

The similar results between the current experiment and Experiment 8 (i.e., with facial properties) indicate that the effects were unrelated to the social signals resulting from the gaze shifts. Instead, these results were likely caused by the geometric properties of the fixation shift in which the direction of the shift (i.e., from center-to-periphery or from periphery-to-center) is inconsequential. Compared to the saccadic responses in Experiment 9, in which fixation shifts caused a facilitation pattern similar to conditions in which the fixation disappeared, the manual responses were inhibited by the fixation shifts, resulting in the elimination of the general warning effect that was expected to occur as a result of the shift in fixation stimulus. This difference between saccadic and manual responses is to be expected if one assumes that the two

responses have different underlying mechanisms. In saccadic reactions, because the displacement and disappearance of a fixation stimulus can neutralize previously activated fixation neurons and result in disinhibition of saccade-generating neurons in the SC, displacement of a fixation stimulus should be sufficient to cause the oculomotor-specific fixation offset effect. By contrast, because manual reactions are affected more by higher perceptual and cognitive information related to the fixation stimulus, there is a possibility that attention disengagement will fail in the vertical shift conditions as a result of the special attention that follows the fixation and that takes place independently from eye movement. Thus, the observed differences between the saccadic and manual responses are consistent with those in previous studies.

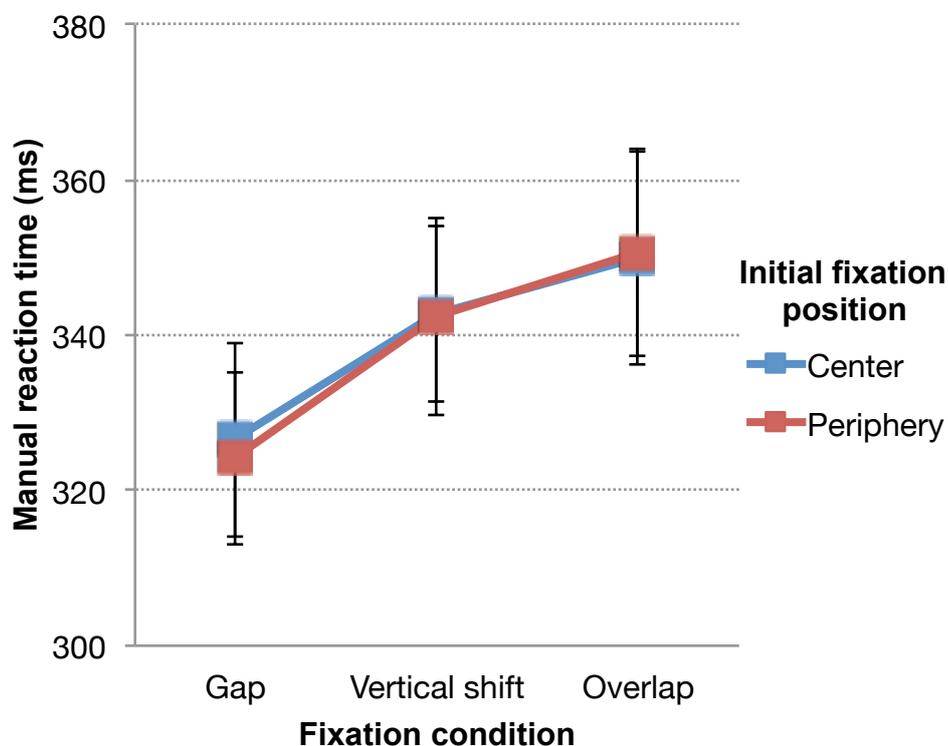


Figure 18. Mean MRTs in Experiment 10. Error bars represent the between-subject standard error of the mean.

Table 4. Mean MRTs (ms) in Experiment 10

Initial fixation position	Fixation condition		
	Gap	Vertical shift	Overlap
Center	327	343	350
Periphery	324	342	351

4.6 EXPERIMENT 11: EFFECTS OF GAZE SHIFT FROM AVERTED TO DIRECT VS. A SUDDEN DIRECT-GAZE APPEARANCE ON SACCADIC RESPONSES

Experiment 7 showed that the shift from an averted to a direct gaze (i.e., the appearance of eye contact) delayed the subsequent saccadic response. Experiment 11 tested whether the shift from an averted to a direct gaze causes a delayed response, or whether the appearance of a direct gaze is sufficient to cause a delayed saccadic response. In this experiment, eyes with no pupils were initially presented, and then the direct or averted gaze abruptly appeared before the target onset.

Methods

Ten new paid volunteers (five men and five women, aged 19–24 years) participated in the experiment. All had normal or corrected-to-normal vision, and normal oculomotor and eye-hand coordination functions. All participants gave written informed consent prior to participation.

The same facial fixation stimulus as Experiment 7 was used, except that the pupils were not displayed during the initial fixation period (see Figure 19). The observers were asked to fixate on the eyes of the face rather than the face as a whole. The pupils of the eyes appeared either in the center (i.e., direct gaze) or in the upper/lower periphery of the sclera (i.e., averted gaze) 200 ms before the target presentation. The rest of the stimuli and procedures were identical to those described in Experiment 7.

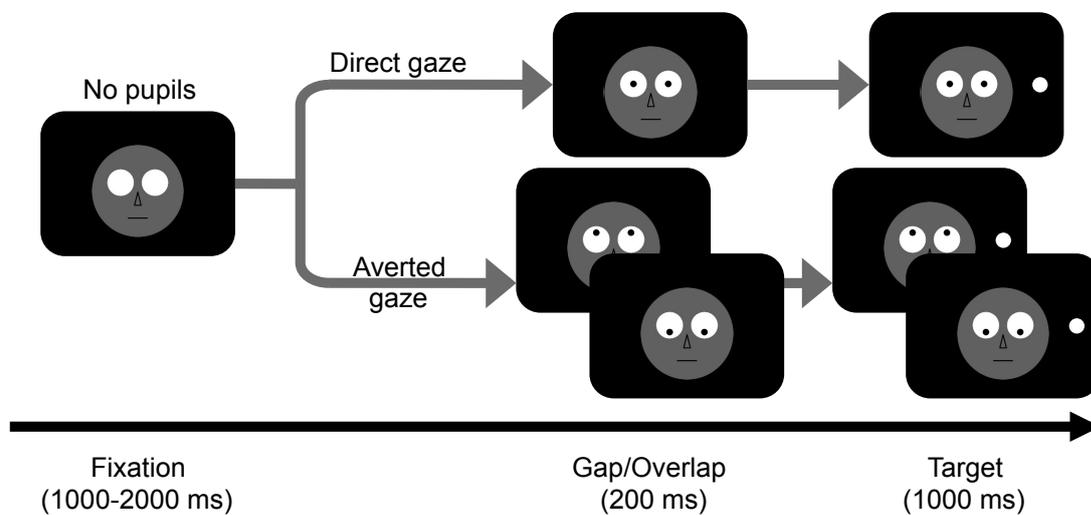


Figure 19. Schematic illustration of the trial sequences in Experiment 11. The same face as Experiment 7 without the pupils was used as the fixation stimulus. The pupils of the face appeared either in the center (direct gaze) or in the upper/lower periphery (averted gaze) of the sclera 200 ms before the target onset. The rest of the stimuli and procedures were identical to those in Experiment 7.

Results and Discussion

The results of Experiment 11 are depicted in Figure 20. Unlike the gaze-shift conditions in Experiment 7, the SRTs following the abrupt onset of a direct and averted gaze were comparable (219 ms and 214 ms, respectively: $t(1,9) = 1.12$, $p = 0.29$). Therefore, the shift from an averted gaze to a direct gaze, rather than the appearance of

a direct gaze per se, interfered with response facilitation in the gap paradigm in Experiment 7.

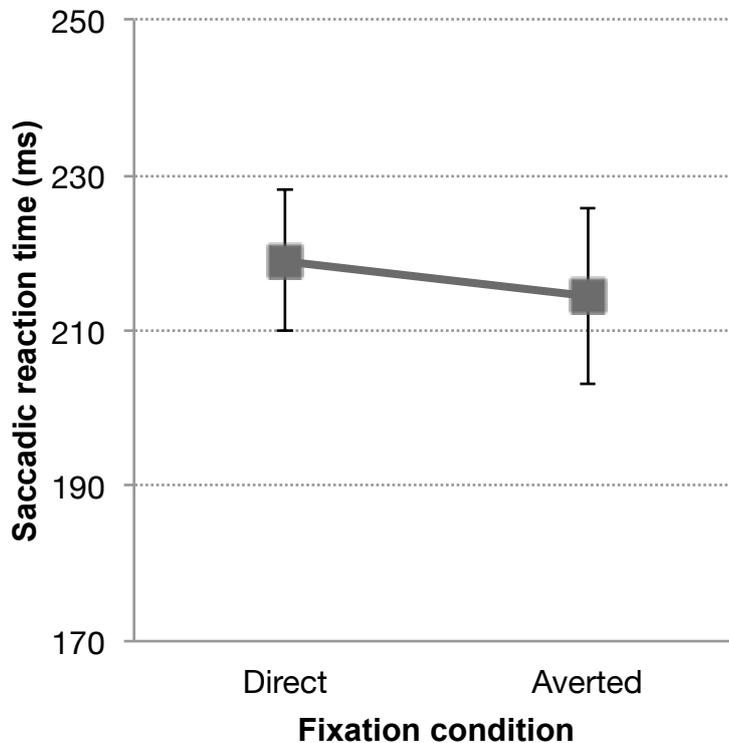


Figure 20. Mean SRTs in Experiment 11. Error bars represent the between-subject standard error of the mean.

4.7 GENERAL DISCUSSION

Study 3 demonstrated that the shift in gaze direction of a facial stimulus on which participants focused shortly before a target onset differentially affected the reaction times of subsequent target-elicited saccadic and manual responses. For saccadic responses, while the disappearance of eye contact between an observer and the facial fixation stimulus facilitated the saccade response in a manner similar to the gap effect, the appearance of eye contact caused no response facilitation (Experiment 7). The

control experiment regarding the geometric factors of the fixation stimulus (Experiment 9) revealed that vertical displacement of the fixated point by itself could induce response facilitation regardless of the shift direction (i.e., from center-to-periphery vs. from periphery-to-center). These results, therefore, indicate that stimulus factors, but not social factors (i.e., eye gaze), are responsible for the response facilitation caused by the disappearance of a direct gaze in Experiment 7. The results also indicate that the social eye-contact signal was responsible for the response inhibition caused by the appearance of direct gaze in Experiment 7 (which eliminated both the general warning effect and the fixation offset effect). The results of Experiment 11 suggest that this inhibition effect occurred as a result of the shift in gaze from averted to direct, but not as a result of the abrupt appearance of a direct gaze prior to target onset. By contrast, for manual responses, there was no effect of the social signals from the eyes; both gaze shifts inhibited the subsequent manual reactions (Experiment 8). This response inhibition could be attributable to the physical factors of the fixation stimulus (i.e., the shift of the pupil dots) rather than to social factors related to the gaze-fixation stimulus (Experiment 10).

The main finding of Study 3 is that interpretation of the fixation stimulus, particularly the perception of another's gaze, can modulate saccadic facilitation in the gap paradigm. Specifically, shift of the fixation stimulus from an averted to a direct gaze (i.e., making eye contact) eliminated the response facilitation predicted to occur in the gap effect. Study 1 (Chapter 2) demonstrated that the subjective interpretations of a

fixation stimulus could also affect the gap effect (Ueda et al., 2013). Thus, although the direct causes of the gap effect are thought to be automatic processes such as fixation offset or attentional disengagement, the present results suggest that these processes interact with a wider range of processes than were previously considered.

Direct gaze (or eye contact) has a special meaning to humans. Eye contact is known to convey a wealth of non-verbal information, which is fundamental for social interactions and communications (Emery, 2000; Kleinke, 1986). Eye contact has been shown to affect both perceptual and cognitive processes, leading to a higher sensitivity to direct gazes. For instance, people are particularly good at finding a 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). A recent study has also observed higher sensitivity to direct gaze in unconscious processes, in which a face with a direct gaze broke the state of interocular suppression (i.e., invisibility) faster than did a face with an averted gaze (Stein, Senju, Peelen, & Sterzer, 2011). Therefore, the processes underlying gaze perception are rapid and implicit (for reviews, see Johnson, 2005; Senju & Johnson, 2009). The current results indicate that the transition from an averted to a direct gaze induces the automatic attraction of attention, which overcomes the facilitation effect by physical translation of the fixation points. Although the precise underlying mechanisms could not be revealed by the present experiments, it is possible

that facilitation caused by transition of the fixation point is prevented by the failure of attentional disengagement/shift due to the signal from the averted-to-direct gaze shift.

Furthermore, the results of Experiment 11 revealed that the response inhibition caused by eye contact is specific to the shift of gaze direction; while the abrupt appearance of direct and averted gazes caused no difference on the SRTs (Experiment 11), the transition from an averted to a direct gaze and from a direct to an averted gaze caused a significant difference in the SRTs (Experiment 7). This indicates that inhibition by direct gaze may reflect the processes related to the perception of gaze dynamics. The change in the gaze direction from the averted to the direct gaze has been shown to elicit strong activity in the cortical gaze processing area of the superior temporal sulcus (Pelphrey, Viola, & McCarthy, 2004), and captures spatial attention (Yokoyama, Ishibashi, Hongoh, & Kita, 2011). In addition, gaze shifting is more natural than is the abrupt appearance of a gaze in terms of daily experiences. Thus, while the static image of the face with a direct gaze was not strong enough to inhibit the initiation of the subsequent saccade, the shift of the averted-to-direct gaze might cause a stronger engagement of observers' attention, and result in the failure of the process of the attentional shift.

The difference in the effect of vertical shift of a fixation stimulus between saccadic (Experiment 9) and manual (Experiment 10) responses is also noteworthy. In the saccadic response tasks (Experiment 9), the vertical shift of the fixation stimulus caused response facilitation, which was comparable to that of the fixation offset condition (i.e.,

the gap effect). In contrast, in the manual reaction tasks (Experiment 10), the vertical shift condition inhibited response facilitation by the general warning effect yielding a comparable MRT with that of the overlap condition. This difference in the effects of the vertical shift fixation might be attributed to differences in the underlying mechanisms of the saccadic and the manual gap effects. More specifically, the oculomotor-specific fixation offset effect affects only the saccadic gap effect but not the manual gap effect. Regarding the two putative components of the gap effect (i.e., the fixation offset effect and attentional predisengagement), attentional predisengagement should occur equally in the vertical shift condition of the saccadic and manual tasks. If so, the only component that could cause the different effects on the saccadic and manual responses is the presence of the fixation offset effect. This explanation is plausible because a sufficient condition for the fixation offset effect is the deactivation of the fixation-related neurons. This condition would likely be met by the displacement of the fixation stimulus from the fixating location.

In summary, the present study demonstrated that a relatively higher cognitive process, the perception of change in gaze direction, can modulate the saccadic gap effect. This result highlights the special property of gaze direction, in that it can potentially inhibit the oculomotor-specific fixation offset effect. Furthermore, these results indicate that the fixation offset effect is not likely to contribute to the manual gap effect; thus, the manual gap effect does not arise from the same mechanism as the saccadic gap effect. Further studies should address what mechanisms are responsible for

rendering the saccadic gap effect ineffective when another person's eye contact is perceived.

CHAPTER

5

Conclusion

The present group of studies aimed to determine the contributions of physical inputs and perceptual representation of a fixation stimulus on the saccadic and manual gap effects by taking advantage of phenomena of visual perception, specifically amodal completion (Chapter 2) and interocular suppression (Chapter 3). These findings have significant relevance for understanding the two competing hypotheses regarding the fixation-disappearance-specific components of the gap effect (i.e., the fixation offset effect and attentional predisengagement theory). The fixation offset effect posits that the main cause of response facilitation is the physical disappearance of the fixation stimulus, whereas the attentional disengagement theory posits that the main cause is lack of attentional disengagement from the fixation location. Hence, for the latter hypothesis, the subjective disappearance of the fixation stimulus should be sufficient to result in response facilitation. This study pitted these two accounts against one another by revealing the contributions of the physical and subjective disappearance of the fixation stimulus on response facilitation. Each study is summarized below.

Study 1 (Chapter 2) investigated the effects of the physical disappearance and subjective maintenance of a fixation stimulus on the saccadic and manual gap effects.

An occluded fixation point was created by covering the fixation stimulus with a moving mask 200 ms before the target onset in order to produce an anticipatory effect of the maintenance and reappearance of the fixation point. The results indicated that the occluded fixation stimulus partially reduced the saccadic gap effect and completely reduced the manual gap effect. This indicates that the subjective as well as physical disappearance of the fixation stimulus is necessary to induce the saccadic gap effect, whereas only the subjective disappearance of the fixation stimulus may be sufficient to induce the manual gap effect.

In Study 2 (Chapter 3), the necessity of the physical disappearance of the fixation stimulus on the saccadic and manual gap effects was tested. An interocularly suppressed (invisible) fixation point was used. The results demonstrated that physical maintenance of an invisible fixation stimulus slightly but significantly reduced the saccadic gap effect but not the manual gap effect. Thus, combined with the results of Study 1, these results indicate that the saccadic gap effect occurs only when the fixation stimulus disappears both physically and subjectively, whereas the manual gap effect is strongly correlated with the subjective representation of a fixation stimulus. Furthermore, the results also indicate that the saccadic and manual gap effects arise from at least partially different mechanisms. In particular, unconscious processes seem to modulate an oculomotor-specific component of the saccadic gap effect, presumably via subcortical mechanisms.

Study 3 (Chapter 4) examined the effects of social signals from a gaze-fixation stimulus on the saccadic and manual gap effects. To investigate the effect of higher cognitive functions, a facial fixation stimulus, which is often used in developmental and clinical psychology, was tested. The results demonstrated that higher cognitive functions, particularly the perception of another person's gaze, differently modulate saccadic and manual facilitation in the gap paradigm. For saccadic responses, while the disappearance of eye contact between an observer and the facial fixation stimulus did not facilitate the saccade response more than the physical displacement of the fixation stimulus did, the appearance of eye contact caused strong response inhibition, resulting in the elimination of the general warning effect that was expected to occur as a result of the shift in the pupils dots. By contrast, for manual responses, there was no effect of the social signals from the eyes; both gaze shifts inhibited the subsequent manual reactions. This response inhibition could be attributable to the physical factors of the fixation stimulus (i.e., the shift of the pupil dots) rather than to social factors related to the gaze-fixation stimulus. The results demonstrated that even higher cognitive functions, particularly the perception of another person's gaze, can modulate saccadic facilitation in the gap paradigm. Moreover, the effect of the geometric properties associated with the gaze shift, particularly the shift of the fixation stimulus, further highlights the difference between the saccadic and manual gap effects. That is, the shift of the fixation stimulus induces the saccadic gap effect but inhibits the manual gap effect.

The findings of the present study will have significant relevance not only in the understanding of the underlying mechanisms of the gap effect, but also in the other areas of studies. First, because of the characteristics of the gap effect, such as robustness of the effect and easiness of the task, it could be an indicator for neurological diseases. The magnitude of response facilitation by the gap effect reach approximately 100 ms, and is insusceptible to the visual properties of stimuli, including a target (e.g., Jin & Reeves, 2009; Reuter-Lorenz et al., 1991; Vernet et al., 2009). The task of the gap-overlap paradigm is simple enough that allows observing the gap effect in people from children to the elderly (Fischer et al., 1993; Munoz et al., 1998; Vernet et al., 2009) and even in non-human primates (Dorris & Munoz, 1995; Fischer & Boch, 1983; Kano et al., 2011). In addition, as in the results of the present study, the gap effect, especially the saccadic gap effect, has both motor and cognitive components; i.e., fixation offset effect and attentional predisengagement, respectively. Therefore, the findings of the present study provide further knowledge regarding the proper use of the saccadic and manual gap effects as a means of screening motor and cognitive neurological disorders, such as amyotrophic lateral sclerosis (ALS), autistic spectrum disorder (ASD), and attention deficit hyperactivity disorder (ADHD). Furthermore, the results of the preset study indicate different means should be used to convey visual information (by foveation) and to prompt motor response. Because physical offset of a fixation stimulus further facilitates the subsequent saccade to a new location, disappearance of the fixated object could also facilitate to convey visual information at a new location to an observer (e.g., Huestegge & Koch, 2010). This would be applicable,

for example, to notify oncoming traffic when a driver is looking at the glass cockpit or car navigation system by turning their display off. In contrast, presenting a warning tone (i.e., general warning effect) is sufficient to prompt a subsequent motor action. Finally, the results of the presents study also elucidated that the target-elicited saccadic and motor responses would be mediated at the different levels of neural mechanisms. In particular, the saccadic response, especially in the gap condition, occurs in a relatively automatic, reflexive manner as compared to the manual responses. This knowledge would be critical for the development of eye-gaze interface of human-computer interaction because disappearance of fixated objects might cause inappropriate response when making a judgment. Therefore, the findings of the present study will be applicable to a wide range of areas in society.

In conclusion, the results of the present series of studies demonstrate that the saccadic gap effect is primarily caused by the oculomotor-specific fixation offset effect, although its magnitude may be reduced by higher perceptual and cognitive functions, including attentional and social components. By contrast, the manual gap effect is presumably mediated by the different mechanisms. In particular, the manual gap effect largely depends on cortical mechanisms, rather than the subcortical mechanisms that underlie the saccadic gap effect. The results of the present experiments alone do not specify the exact components of the gap effects. However, these results do indicate that partially different processes mediate the saccadic and manual gap effects. Moreover, the dependence of unconscious information observed only in the saccadic gap effect can be

considered evidence for the oculomotor-specific component in the gap effect. Further investigation on the neural substrates of the present paradigms should reveal how these mechanisms interact to achieve an efficient response when a fixated stimulus disappears.

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