博士論文

Underlying spatiotemporal structures in human chase and escape behaviors

（ヒトの追跡および逃避行動に潜む時空間的構造）

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Chapter 1

Introduction

Chapter 1: Introduction

“Dexterity (Lovkost)” is a derivative word from the “hunt (Lov)”, and originally a term that refers to the ability of animals to catch prey (Bernstein, 1967). As this word suggests, it has long been thought that “chase behavior”, in which pursuers catch targets, is accomplished by highly sophisticated sensorimotor systems. In fact, the chase behavior, which comprise perceptual detection, localization, and interception of moving objects, is found only among arthropods, mollusks and chordates (Olberg, Worthington, & Venator, 2000). On the other hand, “escape behavior” has been often regarded as a simple action that is released upon presentation of specific stimuli. Recently, however, it has also been considered to be performed by complex cognitive processes that rely on the integration of sensory inputs, prior knowledge, and internal states (Evans, Stempel, Vale, & Branco, 2019).

These chase and escape behaviors are crucial for survival in many animal species, and therefore are fast and robust by necessity, making them incredibly rich subjects in order to investigate the sensorimotor controls of the animals (Card, 2012; Evans et al., 2019). From this background, numerous studies have been conducted so far to investigate chase and escape behaviors in a wide range of animal species. However, these are complex phenomena in which the two agents interact in environments which change from moment to moment, and there are still many unclear points. In Chapter 1, I review previous studies relevant to the chase and escape behaviors in non-humans (Chapter 1.1) and in humans (Chapter 1.2) focusing on the rules underlying chase and escape behaviors. Then, based on the review, I will raise research questions to be answered in this thesis, and present the purpose of this thesis.

1.1 Chase-and-escape behaviors in non-human

1.1.1 Chase strategy

Acquisition of food in many animal species depends on the pursuit and capture of moving prey (Ghose, Horiuchi, Krishnaprasad, & Moss, 2006). To explore how a pursuer captures a target, many researchers have observed positions of pursuers and targets (evaders) during pursuits, and “chase strategy[1]” has been estimated based on these position series. Specifically, these studies compare the behavioral observations with the predictions by the proposed mathematical models and, the chase strategy employed by the animal is inferred from a good agreement between them. As far, three predominant strategies[2], which might be adopted to catch a moving target such as a fleeing prey, have been proposed, and therefore I here outline each strategy.

1.1.1.1 Classical pursuit strategy

The first strategy is classical pursuit (also called “tracking”, “pure pursuit”, or “pursuit”). In the classical pursuit strategy, the pursuer aims at the perceived location of the target. That is, the pursuer moves straightly toward the perceived location of the target at each time. Assuming that the pursuer’s head is fixed, this strategy can be regarded as a steer that minimize the deviation of the image of the target from straight ahead in its visual field (Olberg et al., 2000), and this has the advantage that the pursuer can visually detect the target at the center of the retina with high resolution. If the pursuer moves faster than the pursued (target), this strategy will lead to interception although it yields a curved path

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[1] The “strategy” here refers to the rules that determine which direction a pursuer moves relative to a target at each moment during a pursuit, and the movement speed is generally assumed to be constant for simplicity.

[2] Note that the “strategy” and the “model” are often treated as synonyms in the context of the chase behaviors.

in some conditions where a target moves (Figure1-1). Most insects which have been studied use this simple strategy to pursue moving objects, whether those objects are conspecifics (Land, 1993; Land & Collett, 1974), prey (Gilbert 1997), or artificial objects (Srinivasan & Xiang, 1990), and whether the objects are in the air or on the ground. Behaviors consistent with the classical pursuit model have been observed in houseflies (Land & Collett, 1974), blowflies (Boeddeker & Egelhaaf, 2003), honeybees (Gries & Koeniger, 1996), and tiger beetles (Gilbert, 1997; Haselsteiner, Gilbert, & Wang, 2014).

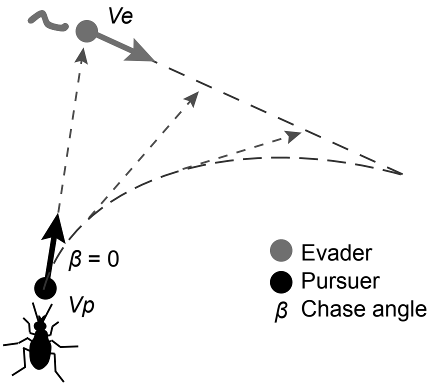

Figure 1-1 Classical pursuit strategy

Pursuit of a target moving in a straight line. The target (gray disc) moves at a constant velocity and the pursuer (black disc) moves at a constant speed. The pursuer moves at the perceived target location in each time, and the chase angle is always zero degrees if there is no visuo-motor delay. (Cited and Modified from Haselsteiner et al., 2014)

1.1.1.2 Time-optimal strategy

The second strategy is time-optimal (also called “interception”, “constant bearing”, or “constant bearing decreasing range”) in which a pursuer moves so as to intercept a target in the minimum time when the situation where target and pursuer move at constant velocity (Ghose et al., 2006; Nahin, 2012). That is, in the time-optimal strategy, the pursuer projects movement path of the target using the perceived location and velocity of the target and aims at the point which intersects the projected movement paths considering the own location and movement speed (magnitude of velocity) (Figure 1-2a), and this yields a relatively straight path of the pursuer compared with the classical pursuit (compare Figure 1-2a with 1-1). This steering law can be realized by the pursuer's maneuvering to maintain the image of evader at a constant angle and the image expand in its visual field when its head is fixed and they move at constant velocity (Kane & Zamani, 2014). Wide range of animals which have been studied use this strategy to intercept moving objects, such as prey or a piece of food sinking in water. Behaviors consistent with the time-optimal model have been observed in teleost fish (Lanchester & Mark, 1975), salamanders (Borghuis & Leonardo, 2015), falcons (Kane & Zamani, 2014), and goshawks (Kane, Fulton, & Rosenthal, 2015).

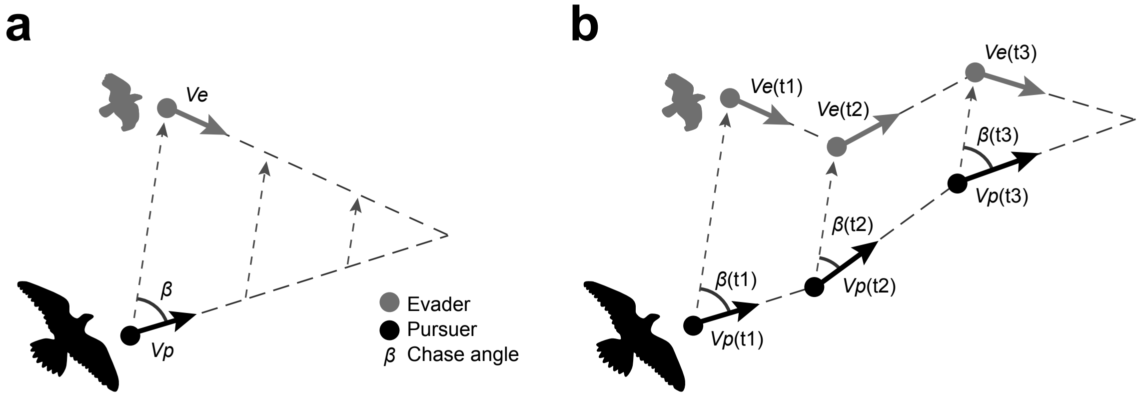

Figure 1-2 Time-optimal strategy

(a) Interception of a target moving in a straight line. The target (gray disc) moves at a constant velocity and the pursuer (black disc) moves at a constant speed (magnitude of velocity). The chase angle is computed so that the pursuer moves along the shortest interception path (see Chapter 2 for details of calculation procedure). Assuming that the pursuer's head is fixed relative to the movement direction, the image of the evader at a constant angle and the image expand in the pursuer's visual field (the dashed arrows from the pursuer to the evader are parallel and their length decreases over time). (b) Interception of an erratically moving target. The target moves erratically, changing both speed and direction. The erratic target motion can be broken into short linear segments. The pursuer moves the local shortest interception path in each segment. (Cited and Modified from Kane & Zamani, 2014)

1.1.1.3 Parallel navigation strategy

The third strategy is parallel navigation (also called "motion camouflage" or "constant absolute target direction"), in which a pursuer approaches the target while maintaining the original target direction in an absolute coordinate system (or compass). That is, also in the parallel navigation strategy, the pursuer can achieve the interception of a target by steering to keep the evader's apparent position on the pursuer's visual field at a fixed angle when the pursuer's head is maintained at a constant angle. This strategy can be interpreted that the pursuer maneuvers to reduce parallax-based cues on the evader's visual field (Justh & Krishnaprasad, 2006; Reddy, Justh, & Krishnaprasad, 2007). In other words, maintaining a constant absolute angle also results in the pursuer being stationary with respect to the background from the viewpoint of the target. This lack of relative motion results in "motion camouflage". This strategy includes the case where there is no decrease in distance depending on the literature (Figure 1-3b). When it is limited to the case where the distance decreases, in situations where an evader moves in approximately linear trajectories, this third strategy is similar to the second strategy (time-optimal strategy) (see Figure 1-2a). On the other hand, in situations where an evader moves erratically, these two strategies can be distinguished because the absolute target direction is disturbed by visuo-motor delay of the pursuer. Behaviors consistent with the parallel navigation model have been observed in dragonflies (Mischiati et al., 2014; Olberg, Seaman, Coats, & Henry, 2007; Olberg et al., 2000; Olberg, 2012) and bats (Ghose et al., 2006).

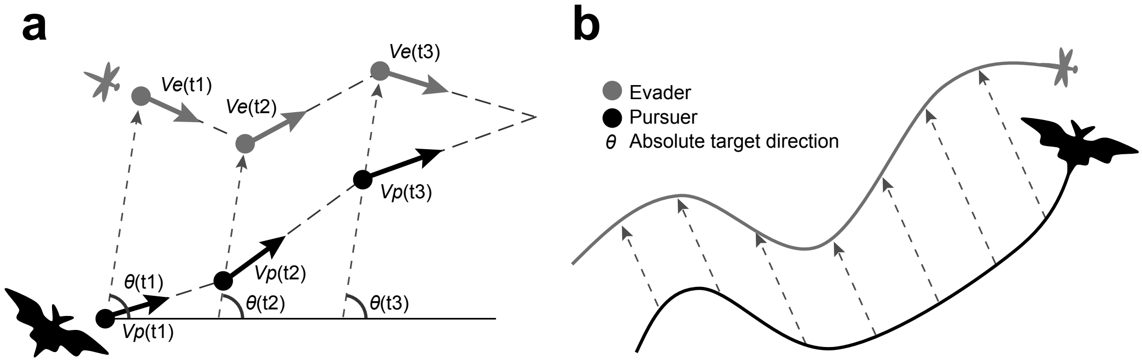

Figure 1-3 Parallel navigation strategy

(a) Interception of an erratically moving target. The target moves erratically, changing both speed and direction. The pursuer moves so as to decrease the distance to the target while the absolute target direction maintained at a constant. (b) An example where the absolute target direction is maintained at a constant but the distance between the pursuer and the target does not necessarily decrease. Some literature includes such behavior in parallel navigation. (Cited and Modified from Ghose et al., 2006, 2009)

In summary, previous studies have proposed three strategies to intercept a moving target, such as fleeing prey. The proposed models have been well consistent with the chase behaviors of many animals, and the chase strategy of the animals have been predominantly categorized into one of them.

1.1.2 Escape strategy

Escape behaviors are used by many taxa as their main defense against predator attacks[3] (Bullock, 1984). In the behaviors, whether an animal successfully avoids predation largely depends on the speed and accuracy of the response behaviors (Eaton, 1984). In order to investigate how the quick and accurate sensorimotor controls is accomplished, previous studies have mainly focused on escape behaviors of insects because they have comparatively tractable nervous systems and are amenable to manipulation with genetic tools. In general, these previous studies have examined escape behaviors responding to the stimulus, and have shown some similarities regarding the initial phase of the escape behaviors among taxa. Here I introduce the findings of the escape behaviors in non-human animals.

1.1.2.1 Away response against stimulus

In general, "directionality" is defined for "away" and "towards" responses, which is based on the direction of the initial rotation (or body bend in flexible animals such as fish (Blaxter & Batty, 1987)) of an escape response relative to the stimulation (Comer & Dowd, 1987; Domenici & Blake, 1993)[4]. It has been known that animals (evaders) often

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[3] A number of defense strategies such as freezing can be used by prey (Eilam, 2005), although these are beyond the scope of this thesis.

[4] Away responses are escapes with a rotation directed away from the stimulus and

show away response against the threat whether it is wind, sound, visual stimulus, tactile stimulus or real predator in a number of taxa, particularly in invertebrates and lower vertebrates. Specifically, the number of the away response exceeds that of the towards response in copepods (Camhi, Tom, & Volman, 1978; Comer & Dowd, 1987; Suchman, 2000), crickets (Kanou, Ohshima, & Inoue, 1999, 2004; Tauber & Camhi, 1995), locusts (Santer, Yamawaki, Rind, & Simmons, 2005), shrimps (Arnott, Neil, & Ansell, 1999), crabs (Nalbach, 1990), frog (King & Comer, 1996), lizards (Martín & López, 1996), Angelfish (Domenici & Blake, 1993), Goldfish (Eaton, Robert & Nissanov, 1985), Herring (Blaxter & Batty, 1987). In addition, the subsequent movement direction relative to the stimulus (often called "escape angle"), often distribute in the direction away from the stimulus in many species, such as, cockroaches (Domenici, Booth, Blagburn, & Bacon, 2008), crickets (Kanou et al., 1999; Tauber & Camhi, 1995), locusts (Santer et al., 2005), and fly (Card & Dickinson, 2008).

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towards responses are escapes with a rotation directed towards the stimulus. As a result, a towards response does not necessarily mean that the final escape direction is towards the stimulus. For example, an animal initially oriented at 170 degrees that makes a 20 degrees rotation towards the stimulus will end up having an escape direction of 150 degrees from the stimulus.

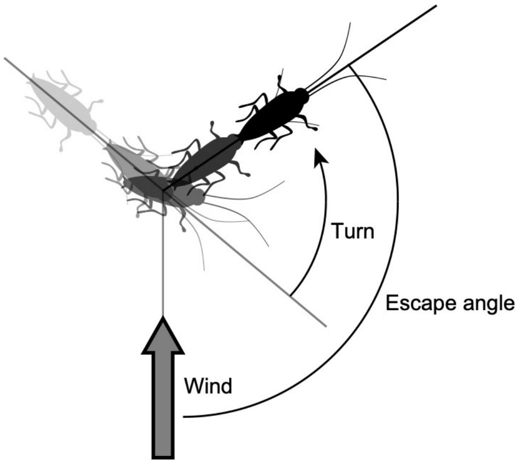

Figure 1-4 Escape response against stimulus

Illustration of the sequence of movements in a typical cockroach escape response. The cockroach is walking from the left to the right of the diagram. The gray arrow indicates stimulus direction. Escape angle is defined as the angle between the stimulus (wind) and the movement direction of the escape cockroach. As shown in this example, when the initial rotation (turn) relative to the stimulus increases the escape angle (towards 180 degrees), the escape response is regarded as “away response”. Conversely, when the initial rotation decreases the escape angle (towards 0 degrees), it is regarded as “towards response”. It should be noted that the escape angle here is called “escape trajectory (ET)” in the original literature, but I do not use this term in this thesis in order to avoid potential confusion because this term may image a longer sequence of movements in some readers. (Cited and Modified from Domenici et al., 2008)

1.1.2.2 Variability in escape direction

As mentioned above, many animals basically move away from threats. On the other hand, in the escape direction, variability have been often observed (Camhi et al., 1978; Domenici & Blake, 1993; Eaton, Lavender, & Wieland, 1981). For example, repeated observations of the escape behaviors in cockroach against wind showed that the distribution of escape angles was multimodal in individual cockroaches (Figure 1-5) (Domenici et al., 2008). If the evader intends to move toward a fixed escape direction, the distribution of the escape angle should be unimodal, even considering that there are fluctuations in the sensorimotor system. Thus, the multimodal distribution (or variability) showed a possibility that cockroaches increase the unpredictability against predators by varying escape direction (Domenici et al., 2008). It should be noted that most observed escape angles were within the 90-180 degrees. That is, if cockroaches maximize the unpredictability by choosing the escape direction at completely random, some escapes will be directed towards the predator and decrease the chance of survival (Domenici et al., 2008). As a result, these suggest that cockroaches employ an advantageous middle-ground strategy where the escape direction is selected from a set of possible movement direction.

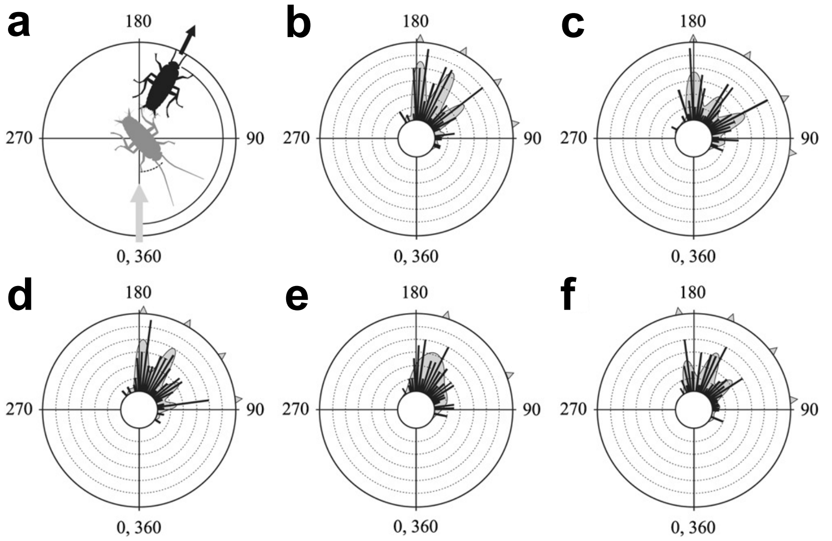

Figure 1-5 Multimodal distributions of escape angles

(a) Illustration of the definition of escape angle. The escape angle (continuous arc) is defined as the angle between the wind direction (gray arrow) and the movement direction (black arrow) of the escaping cockroach (black cockroach). Left and right stimuli were pooled as if each stimulus was always on the right side of the animal. (b to f) The frequency distributions of five individual cockroaches tested in repeated trials. Numbers of responses are (b) 93, (c) 93, (d) 89, (e) 81, and (f) 75. Best-fit distributions in (b) to (f) are shown as multimodal curves. (Cited and Modified from Domenici et al., 2008)

1.1.2.3 Geometrical rationality in escape direction

Geometric models have been developed to predict a possible range of escape direction for reaching the safety zone such as shelters (Arnott et al., 1999; Corcoran & Conner, 2016; Domenici, 2002; Weihs & Webb, 1984a). The geometric models regarding the initial escape predict the range of successful escape directions based on the kinematic parameters, such as relative speed of the predator and the prey (Figure 1-6) (Arnott et al., 1999; Domenici, 2002; Weihs & Webb, 1984a). For simplicity, these models assume constant velocity of predator and constant speed of prey. In other words, the predator does not change their movement direction and speed during its attack. In these models, escape angle are considered to range only 0-180 degrees and are defined as the angle between the threat and the escape direction of the animal, with 0 degrees indicating movement towards the threat, 180 degrees movement directly away from the threat and 90 degrees movement perpendicular to the attack of the threat (Domenici, Blagburn, & Bacon, 2011a). Escaping of 180 degrees is considered as a behavior in order to increase the distance from stimulus. This behavior is valid when a speed of prey is faster than or equal to that of threat approaching. On the other hand, when a speed of threat is faster than that of a prey, a prey escaping of 180 degrees would eventually be captured. These simple geometric models provide the solutions for the escape angle needed in order to reach a safety zone before being caught by the predator, and the solutions (predicted escape angles) often distribute within the 90 to 180 degrees sector depending on the relative speed of predator and prey. These predictions are consistent with some behavioral observations, and it suggests that the escape behaviors of animals are geometrically reasonable.

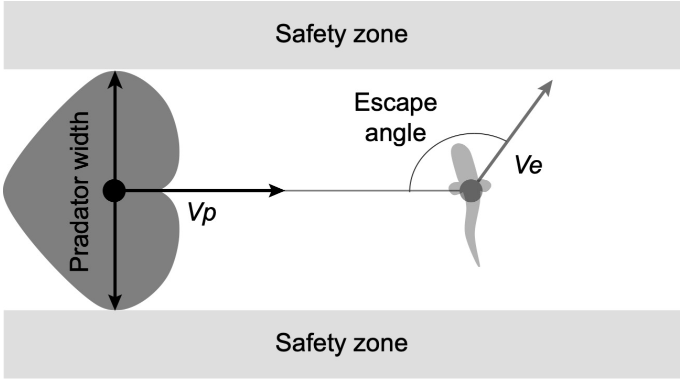

Figure 1-6 Geometric model of initial escape

The shaded area at the top and bottom of the diagram is safety zone for evader. This geometrical model provides the range of the escape angle in which the evader (gray disk) can reach the safety zone before captured by the predator (black disk), corresponding to their kinematic parameters such as predator width, speeds of predator and evader, and the distance between them. (Cited and Modified from Domenici et al., 2002)

In summary, escape behaviors of many animals are basically movement away from stimuli, and this would be reasonable in order to increase the chances of reaching a safety zone. In addition, some organisms may increase the unpredictability against predators by varying their escape directions at this time.

1.2 One-on-one behaviors in sports in human

1.2.1 Skills of perception and action

One approach to study one-on-one behaviors is to focus on the individual skills of the player. In general, the one-on-one behaviors are thought to be complex phenomena in which the cognitive and motor controls of two agents interact. Thus, in this approach, experimental subjects are simplified by cutting out a scene in the game. Specifically, many previous studies have focused on the direction change of the attacker and the response of the defender, and have investigated the individual skills of perception and action.

1.2.1.1 Direction change with deceptive movement

An attacker is often required to pass a defender, and, conversely, the defender required to respond and stop the attacker’s maneuver in ball sports such as football, rugby, and basketball (Fujii, Shinya, Yamashita, Kouzaki, & Oda, 2014; Fujii, Yamashita, Yoshioka, Isaka, & Kouzaki, 2014). One of the effective behaviors of attackers in such a situation is sudden direction change. The sudden direction change could be thought as the exploitation of the extrapolation of the defender by the attacker. In general, there is a delay from sensory input to motor output, and it is inevitable in animals (Franklin & Wolpert, 2011). As a result, it is necessary for interception of a rapidly moving target to compensate the delay. For example, in baseball hitting, if the bat directed to the location of the ball at the time of detection, when the bat arrives that point, the ball will be in the mitt of the catcher. Thus, to intercept a moving target, humans (and many non-human animals as shown in Chapter 1-1) predict a future position of the target by short-term extrapolation using the current position and velocity information of the target, and reach their effectors, such as hand, body, or bat, for the future position (Dessing, Bullock, Peper, & Beek, 2002). In one-on-one behaviors, attackers try to take advantage of the short-term extrapolation of defenders. That is, firstly, attackers move to a certain direction and make the defender extrapolate own (attacker’s) future position, and then they suddenly change their movement direction (Figure 1-7a). This sudden direction changes of attackers are observed in many sports (Brault, Bideau, Craig, & Kulpa, 2010; Brault, Bideau, Kulpa, & Craig, 2012). In addition to the sudden direction changes, the attacker exaggerates the movement of its body parts, such as upper trunk yaw and the out-foot placement to deceive the defender (Figure 1-7b).

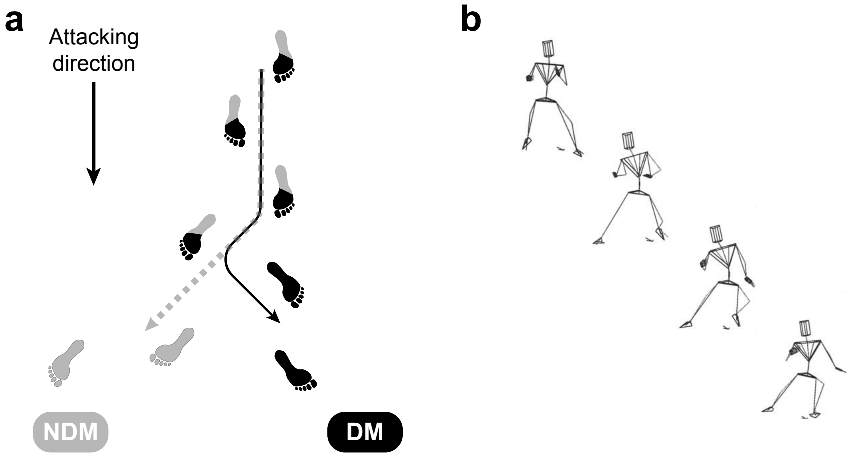

Figure 1-7 Direction change of attacker

(a) Illustration of direction change with a deceptive movement (DM) and without non-deceptive movement (NDM). (b) In the direction change with a deceptive movement, attackers exaggerate the movement of their body parts, such as upper trunk yaw and the out-foot placement. (Cited and Modified from Brault et al., 2010, 2012)

1.2.1.2 Extraction of appropriate perceptual information

Previous studies focusing on the response behaviors of the defender have investigated how accurately and quickly defender respond the direction change with deceptive movements of the attacker using cognitive tasks called occlusion paradigm. In this paradigm, at first, researchers prepare a video of the defender's viewpoint that simulates a situation where an attacker maneuvers to pass a defender during games. Then, the pre-prepared video is displayed to participants simulating a defender, and the participants are asked to reply with oral or response with brief body movement (e.g., side-step) whether an attacker moves leftward or rightward (Figure 1-8).

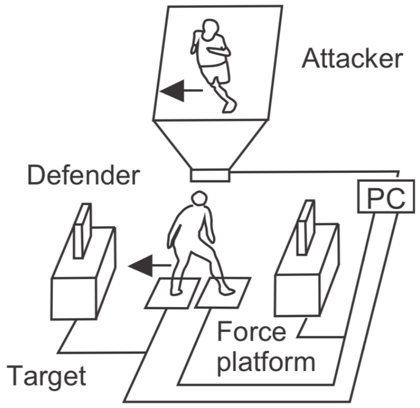

Figure 1-8 Illustration of an experimental setup in occlusion paradigm

The defender (participants) response with side-step to the maneuvers of the attacker (video). (Cited and Modified from Fujii et al., 2014)

This paradigm primarily includes temporal occlusions, spatial occlusions, and combinations of them. In the temporal occlusion paradigm, a series of play video is suddenly occluded at a certain time (the whole screen turns black), and, in the spatial occlusion paradigm, a part of play video such as upper body or lower body is occluded. These paradigms are used to investigate "when" and "where" information is necessary for a correct response (or prediction) of the defender, for experts and novices.

A series of studies have shown that, in general, experts can predict the movement of an opponent quickly (i.e., in the earlier stage of the movement) and accurately[5] (i.e., higher proportion of correct response) (Abernethy, Zawi, & Jackson, 2008; Abreu et al., 2012; Aglioti, Cesari, Romani, & Urgesi, 2008; Brault et al., 2010, 2012; Jackson & Mogan, 2007; Jackson, Warren, & Abernethy, 2006; Lopes, Jacobs, Travieso, & Araújo, 2014; Mori, Ohtani, & Imanaka, 2002; Tomeo, Cesari, Aglioti, & Urgesi, 2013; Wright & Jackson, 2014) . Especially in a study of side-step in rugby, as

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[5] There is a debate whether it is accurate.

mentioned above, an attacker exaggerates the movements of its body parts, such as upper trunk yaw and the out-foot placement in order to deceive the defender in the phase of direction changes (Abernethy et al., 2008; Brault et al., 2010, 2012; Jackson et al., 2006; Wright & Jackson, 2014), but expert defenders can extract and utilize ‘honest’ movement signals (i.e., center of mass) to detect deceptive movement of the attacker (Brault et al., 2012). As a result, they can respond quickly and accurately. On the other hand, novice players are often fooled by ‘deceptive’ movement signals (i.e., exaggerating upper trunk yaw and out-foot placement) and tend to move to the wrong direction (Brault et al., 2012).

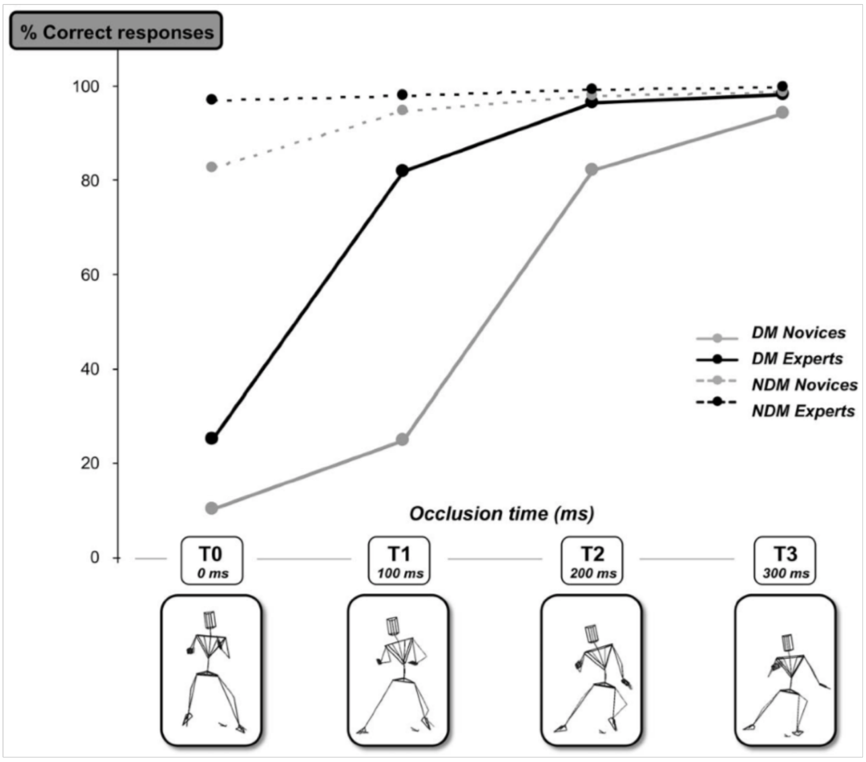

Figure 1-9 Proportion of correct responses

Mean percentage of correct responses for novice (grey line) and expert (black line) groups when presented with deceptive movement (DM – solid line) and non-deceptive movement (NDM – dashed line) at the four different occlusion times (T0, T1, T2, and T3). The stick pictures below represent the differences in body configuration at each occlusion time. (Cited and Modified from Brault et al., 2012)

In summary, the direction change of the attacker and the response to it of the defender is commonly observed in many sports, and these have been investigated mainly in terms of the perceptual and motor skills. In this situation, the attacker suddenly changes its movement direction with exaggerating the movements of its body parts, such as upper trunk yaw and the out-foot placement, in order to deceive the defender. For the direction change with deceptive movements, expert defenders can respond quickly and accurately by extracting the ‘honest’ movement signals, whereas novice defenders tend to move to the wrong direction by using the ‘deceptive’ movement signals

1.2.2 Dynamics of perception and action

Another approach to study one-on-one behaviors is to focus on the dynamics of the attacker and defender. In this approach, one-on-one behaviors are regarded as non-linear dynamical systems, and thus previous studies have dealt interactive one-one-one behaviors, which is often observed in actual games, as experimental subjects from the standpoint that those cannot be broken down into parts. There are two methods to investigate the non-linear dynamics, namely, analytical and theoretical approaches (Jackson, 1991). In analytical approach, the variables that explain complex phenomena are extracted by measurement, and, in theoretical approach, the variables are mathematically estimated by differential equations and difference equations (Strogatz, 2000).

1.2.2.1 Common dynamics in one-on-one behaviors

The previous studies of the analytical approaches have generally recorded interactive one-on-one behaviors and have analyzed the positional coordinates of the attacker and defender in two-dimensional plane[6] (e.g., Figure 1-10). Many variables that describe one-on-one behaviors have been proposed, and one of the variables that well describe is the angle defined by the position of the two agents and the reference frame (Figure 1-11a) (Esteves et al., 2012; Passos, Araújo, Davids, Gouveia, & Serpa, 2006; Travassos, Duarte,

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[6] In most studies, the position coordinates of a player are taken as the center of the head or the point between the foots.

Vilar, Davids, & Araújo, 2012; Vilar, Duarte, Silva, Chow, & Davids, 2014). In these studies, the angle is used as the order parameter, which is characterize the state of the dyadic system. This state is categorized as either being stable or unstable (Figure 1-11b) (Passos, Araújo, & Davids, 2013). A stable state corresponds to a situation in which the attacker and defender are facing each other (the angle is between 0 and 180 degrees). An unstable state corresponds to a situation in which the attacker has broken past the defender (the angle is less than 0 degrees or more than 180 degrees). These studies have shown that successful attack in one-on-one behavior is commonly described as a sudden transition (called phase transition) with a precursor (called critical fluctuation) from the stable state to the unstable state across sports such as football, rugby and basketball (Figure 1-12).

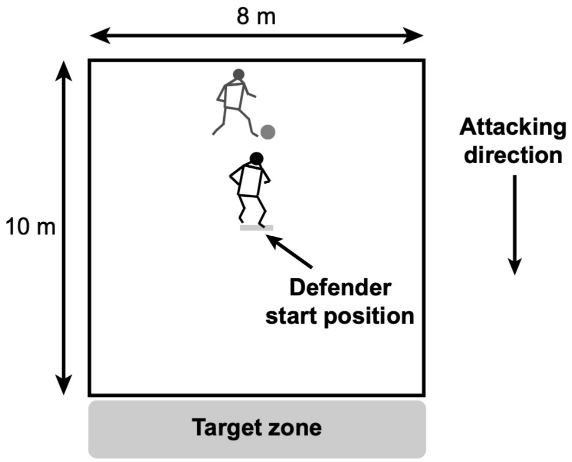

Figure 1-10 Illustration of a one-on-one task

The attacker tried to destabilize a dyad formed with a defender to move into the free space (target zone) behind the defender. Conversely, the defender tried to maintain dyadic stability by recovering and stealing the ball. (Cited and Modified from Duarte et al., 2012)

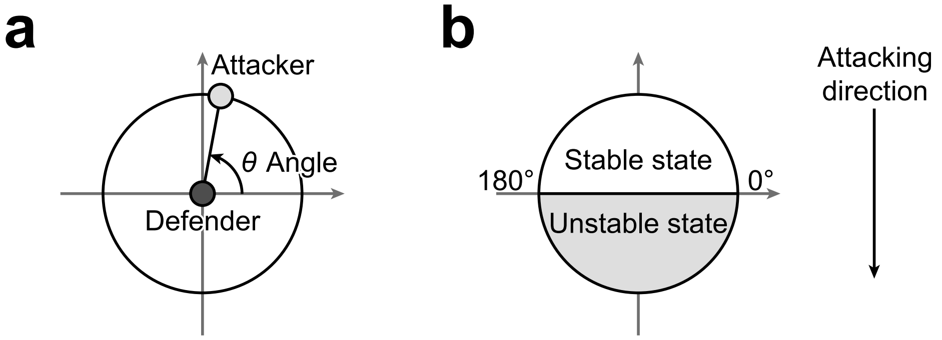

Figure 1-11 Illustration of state of dyadic system

(a) The angle is used as the order parameter, which is characterize the state of the dyadic system. (b) The state is categorized as one of either stable or unstable. The stable state corresponds to a situation in which the attacker and defender are facing each other, and the unstable state corresponds to a situation in which the attacker has broken past the defender.

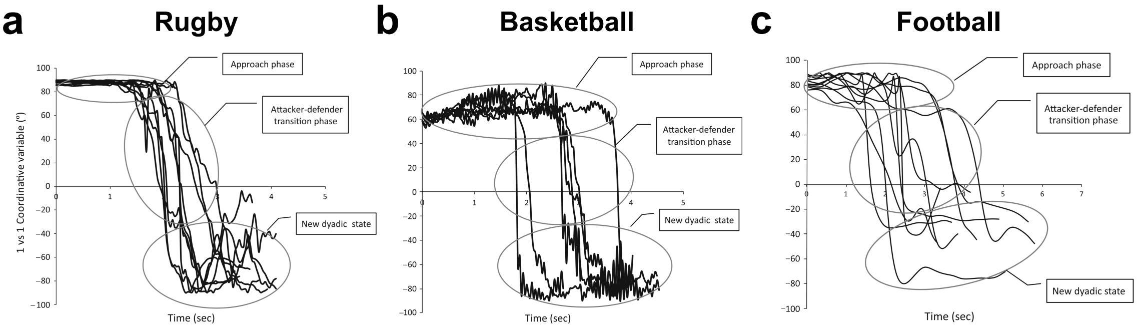

Figure 1-12 Phase transition in one-on-one behavior

(a-c) The sudden transition of the dyadic system from the stable state to the unstable state in (a) rugby, (b) basketball, and (c) football. The approach phase is characterized by positive value of the angle. The attacker-defender transition phase is characterized by zero crossing of the angle. The new dyadic state is characterized by negative values of the angle. (Cited and Modified from Passos et al., 2013)

1.2.2.2 Key parameters in one-on-one behaviors

The previous studies of the theoretical approaches proposed theoretical models, and examined the stability corresponding to the change of two control parameters, which control the order parameter by comparing the change of the potential function and motion equation (Figure 1-13) (Araújo, Diniz, Passos, & Davids, 2014; Davids et al., 2015). This model incorporates the relative velocity and the interpersonal distance as control parameters based on the empirical evidence (Araújo et al., 2014; Fujii, Isaka, Kouzaki, & Yamamoto, 2015; Passos, Araújo, Davids, Gouveia, et al., 2008; Passos et al., 2009; Passos, Araújo, Davids, & Shuttleworth, 2008; Vilar et al., 2014) The potential function is given by

$$V(x) = -k_1x + k_2ax^2/2 - bx^4/4 + x^6/6\,,$$

where k_1 and k_2 are two control parameters, and a and b are two constants given by $a = (\pi/4)^2 \times (\pi/2)^2$, and $b = (\pi/4)^2 + (\pi/2)^2$, $-k_1$ is the relative velocity and k_2 is the interpersonal distance. The motion equation is given by

$$dx/dt = k_1 - k_2ax + bx^3 - x^5 + Q^{0.5}\varepsilon_t\,,$$

where Q is the noise variance and ε_t is white noise. These studies have shown the change of the order state in the dynamics of attacker and defender by the potential function and motion equation incorporating two key parameters, namely, relative velocity and inter-agent distance.

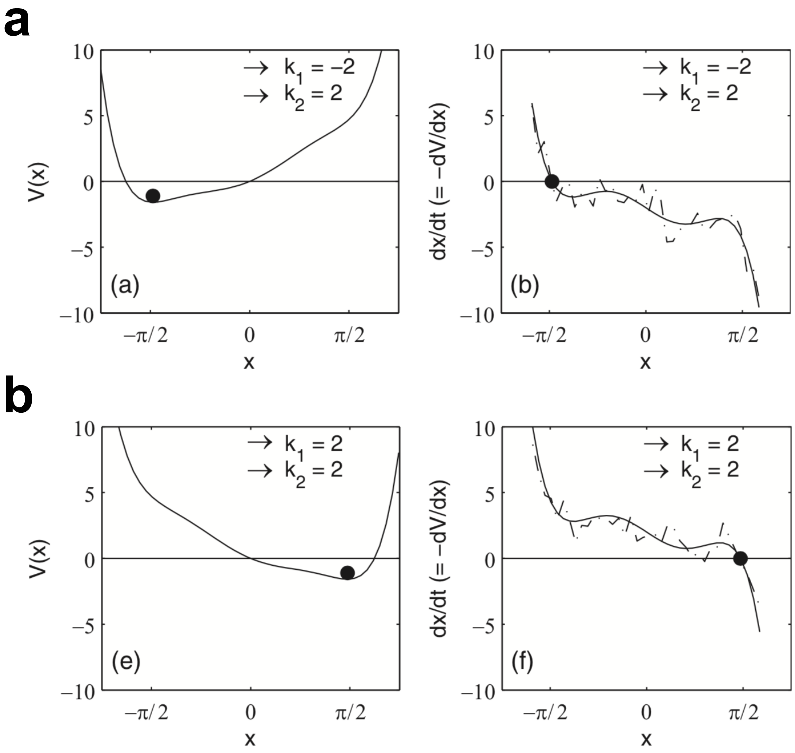

Figure 1-13 Graphical representation of potential function

(a, b) The potential function (the left side) and motion equation (the right side) of one-one-one in rugby. (a) When $k_1 = -2$ (the speed of attacker is greater than that of defender), the attacker passed the defender (clean try). (b) When $k_1 = 2$ (the speed of defender is greater than that of attacker), the defender caught the attacker (effective tackle). (Cited and Modified from Araujo et al., 2014)

In summary, previous studies have applied the dynamical system approach to the one-on-one behaviors in ball sports, and have analytically shown that the state or the outcome of the behaviors of the attacker and the defender can be described by using the angle. Moreover, the previous studies have theoretically presented the potential function and the key variables (i.e., relative velocity and inter-agent distance), which could affect the stability of the dynamics, that is, determinants of one-on-one outcomes.

1.3 Purpose and contents of this thesis

As seen above, previous studies in non-human and in human have accumulated findings regarding the chase-and-escape and one-on-one behaviors. These studies have shown that the interactive behaviors seem to be complex but these are based on some simple rules. That is, the previous studies in non-human have shown that, even if the movement trajectory of the pursuer and the evader in the absolute (global) coordinate system seems to be complex, the behavioral rule could be described as a relatively simple strategy[7] by paying attention to the movement direction in the relative (local) coordinate system. In addition, the previous studies on individual skills have indicated that the direction change of the attacker and the response of the defender are the characteristic behaviors in one-on-one behaviors, and the performance of these behaviors would be a critical for the successful attack and defense. Furthermore, the previous studies applying the dynamical system approach to one-on-one behaviors have shown that there is the common structure in the dynamics of the attacker-defender system across sports events. These studies have presented a wide range of findings from individual strategies and skills to the dynamics of the system behaviors, and these provide many insights into perception and action or learning and evolution. However, there are still unclear points. In particular, the previous studies of dynamical system approach to one-on-one behaviors have mainly investigated the dyadic (attacker-defender) system behavior, and individual behavioral rules of the agents in the system remains unknown. As a result, the relationship between individual behaviors and system behaviors (or successful attack and defense) are also unclear. In addition, the previous studies in non-human have referred the stability and flexibility[8] of

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[7] There are more complex models such that have a time window to integrate sensory information (Bar et al., 2015).

[8] The stability and flexibility are two complementary attributes exhibited in animal

chase and escape behaviors, but it is still largely unknown. Thus, the purpose of this thesis is to comprehensively deepen our understanding of chase-and-escape and one-on-one behaviors for human chase-and-escape interactions.

Firstly, I need to elucidate the human chase strategy in chase-and-escape interactions. Previous studies on chase (defense) behaviors in human have mainly investigated the response behaviors of the defender to the direction change of the attacker. While these studies have shown that the short response time of the defender would be one factor of the successful defense, the scope of these studies have been limited to one dimension (i.e., medio-lateral direction). On the other hand, previous studies on chase behaviors in non-human have proposed the chase strategies, which might be employed, through mathematical modeling of animal behaviors, and these have provided the movement directions of the pursuer in a two-dimensional plane (or three-dimensional space) during chase-and-escape interactions. Thus, in Study 1 (Chapter 2), I investigated the chase strategy of the defender on a two-dimensional plane in order to expand the scope of the human chase behaviors by applying the findings of the chase behaviors in non-human animals.

Secondly, I need to clarify the human escape (i.e., penetration) strategy in chase-and-escape interactions. Previous studies on escape (attack) behaviors in human have investigated the sudden direction change. However, these studies have been fairly limited the movement and its play area, and it is unknown about the movement direction

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behaviors (Warren, 2006). The stability is characterized by that behaviors are consistent over time and reproducible on separate occasions. On the other hand, the flexibility is characterized by that behaviors are not locked into a rigid solution but tailored to current environmental conditions.

and direction change of the attacker in situations where agents can move freely on a two-dimensional plane. Moreover, most of the previous studies relevant to direction changes have focused on the kinematic information of the body part, and little is known the other aspects. For example, the spatiotemporal characteristics such as positions on the court and rhythms on the direction changes may affect the response behaviors of the defender even if the direction change movement itself is the same. Furthermore, the influence of knowledge accumulations (or learning) from repeated competitions is largely unclear. Thus, in Study 2 and 3 (Chapter 3 and 4), I investigated the escape strategy of the attacker in a two-dimensional plane focusing on the movement direction and direction changes.

Thirdly, I need to reveal the relationship between individual behaviors and the system behavior in chase-and-escape interactions. As mentioned above, previous studies of dynamical system approach have focused on the dyadic (attacker-defender) system behavior, and individual behaviors (or strategies) of the agents in the system is unclear. In addition, these studies have presented the theoretical model and the key parameters, which could determine the outcome (successful attack or defense), but there is a lack of observational evidence in controlled experimental conditions. In addition, the theoretical model contains only some of the key parameters, which would affect the outcome, presented by the previous studies, and the relationship among key parameters is unclear. Furthermore, the model (implicitly) assumes that the behaviors (or strategies) of agents would be consistent for the change of parameters, but it has not been confirmed. Thus, in Study 3 (Chapter 4), I investigated the change of individual behaviors and the behavioral outcome by manipulation of the key parameters of the agent.

Fourthly, I need to disclose the effects of environment on individual behaviors and the system behavior in chase-and-escape interactions. While many previous studies have emphasized the importance of the environment surrounding the two agents, most of these studies have investigated the behaviors in a single environment, and the effects of environmental changes on both individual and system behaviors are largely unclear. Thus, in Study 4 (Chapter 5), I investigated the change of individual behaviors and the behavioral outcome by manipulation of spatiotemporal constraints.

Then, in Chapter 6, I integrate and discuss the results obtained from the four studies. Finally, I describe the future directions and the implications to sports of the present findings. Specific problems and research questions to be answered in this thesis are as follows:

Chase strategy: It has been investigated how pursuer capture a fleeing target in many animal species, but human chase strategy is still unclear. How do humans intercept a fleeing target? Also, is there a difference in the strategy between agents who are good at interception and those who are not?

Escape strategy: So far, many previous studies have shown that certain stimulus induce the away response of the evader. Then, how does evader reach to a safety zone behind an opponent? Also, in such situations, evaders (attackers) would make a sudden change of direction and pursuers (defenders) would respond to it. Are there some characteristics for these behaviors?

Determinants of chase-and-escape outcomes: Previous studies have raised several key parameters that may affect the chase-and-escape or one-on-one outcomes, but the relationship among these parameters are unclear. Also, these previous studies have mostly used theoretical approaches, and thus there is a lack of observational study of the actual interactive behavior of the two agents. Does manipulation of a parameter directly change the outcomes of their interactions? Or are adaptive behavioral changes observed corresponding such parameter manipulations?

Behavioral changes due to environmental constraints: Previous studies have focused primarily on the behaviors of agents in chase-and-escape or one-on-one behaviors. Although, recently, these behaviors have been viewed from a broader perspective including the environment surrounding them, many of the recent previous studies are theoretical and there is little observational evidence. Do spatiotemporal constraints, which is major in sports, change human chase and/or escape behaviors? If so, what and how do those change?

Chapter 2 Study 1

Human chase strategy for intercepting an erratically moving target in chase and escape interactions

This study has been published as:

Tsutsui K., Shinya M., and Kudo K. “Human Navigational Strategy for Intercepting an Erratically Moving Target in Chase and Escape Interactions”. *Journal of Motor Behavior*. 0022-2895. 2019.

2.1 Introduction

The ability to pursue and capture moving prey is crucial for the survival of many animals (Brighton, Thomas, & Taylor, 2017; Ghose et al., 2006). Also, for modern humans, pursuit and interception of a moving target are essential skills in a variety of sports (Fajen, Riley, & Turvey, 2009; Shaffer, Dolgov, Maynor, & Reed, 2013). Specifically, in one-on-one situations, a defender is often required to chase and catch an attacker who moves erratically and interactively in ball sports, such as football, rugby, and basketball.

Previous studies on human interception behaviors have mainly investigated conditions where the trajectory of a target is predictable (Chapman, 1968; Kistemaker, Faber, & Beek, 2009; McBeath, Shaffer, & Kaiser, 1995; McLeod & Dienes, 1993, 1996; McLeod, Reed, & Dienes, 2003; Shaffer, McBeath, Roy, & Krauchunas, 2003). For example, in a fly ball catch for outfielders, the trajectory of a fly ball can be predicted as parabolic by Newton's equation of motion[9], although there are disturbances such as air resistance, ball spin, and wind (Marken, 2005; Zago, Matic, Flash, Gomez-Marin, & Lacquaniti, 2018). Many of these studies have referred that the optical information, such as the position of the target relative to the pursuer and the derivatives, is basis of the target interception behaviors.

Recently, interception behaviors have been investigated in other conditions, such as where a pursuer attempted to catch an unpredictably moving target such as a frisbee (Shaffer, Krauchunas, Eddy, & McBeath, 2004a; Shaffer, McBeath, Krauchunas, & Sugar, 2008), toy helicopter (Shaffer, Marken, Dolgov, & Maynor, 2013), or robot

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[9] It should be noted that it does not mean that the pursuer (e.g. outfielder) uses a predictive interception strategy. Previous studies have rather proposed that the pursuer uses an interception strategy based on on-line controls using optical information such as the target direction and the derivatives (There is a debate about the optical information used).

moving on the ground (Wang, McBeath, & Sugar, 2015). These studies have explained the interception of erratically and unpredictably moving targets by dividing the trajectory of the target into short linear segments. This suggests that navigational strategies for intercepting a target under predictable conditions can apply under less predictable conditions. However, it remains unknown how humans intercept a moving target under interactive conditions such as chase-and-escape behaviors.

To address this question, I investigated human navigational strategy in chase-and-escape interactions through mathematical modeling of actual interactive human behaviors. Among several navigational models for catching a target, I focused on classical pursuit, time-optimal, and parallel navigation strategies, which have been predominantly proposed in previous studies of interactive behavior models including non-human animals (e.g., predator-and-prey interactions). The first possible strategy is classical pursuit (also called simply “pursuit”), in which a pursuer moves directly toward the target. Although the classical pursuit strategy allows the pursuer to make contact with the target when the pursuer moves faster than the target, it has been known to be inefficient because it yields a curved path in some conditions where a target moves (Figure 2-1a) (Rushton, Harris, Lloyd, & Wann, 1998). Behaviors consistent with the classical pursuit model have been observed in humans when pursuing a slowly moving target (Rushton et al., 1998). The second alternative strategy is time-optimal, which yields the shortest path to intercept a moving target under the condition that the target moves at constant velocity (direction and magnitude) and the pursuer moves at constant speed (magnitude) (Figure 2-1b). In other words, a pursuer following the time-optimal strategy can intercept the target in minimum time under the above conditions. When a target moves erratically, there is no globally minimum-time interception, and a pursuer follows a local time-optimal path by continually adjusting its own movement according to the target’s movement (Figure 2-1c). Behaviors consistent with the time-optimal model have been observed in humans when intercepting a target moving in a straight line (Fajen & Warren, 2004). The third possible strategy is parallel navigation, in which a pursuer approaches the target while maintaining the original target direction in an absolute coordinate system (or compass). This strategy, as a means to detect a collision course with another object, has long been known to sailors and pilots, and also yields the shortest straight interception path under the condition that the target moves at constant velocity and the pursuer moves at constant speed (Figure 2-1b) (Nahin, 2012; Shneydor, 1998). For this reason, in the predictable condition, the parallel navigation path is similar to the time-optimal path. However, they can differ in less predictable conditions (Wang et al., 2015). Note that the term "bearing angle" was sometimes used to refer to the chase angle β and at other times was used to refer to the absolute target direction θ; thus, to avoid potential confusion, I did not use the term in the present study.

Thus, the objective of our study was to test the possible navigational strategies of humans in chase-and-escape tasks, as seen in ball sports, in both real space and virtual space. The former provides information on interception behaviors in a realistic condition, but it cannot completely control the maximum speed and maneuverability of the pursuer (defender) and the target (attacker). Furthermore, to avoid fatigue I could not include a large number of trials. On the other hand, the latter enables us to confirm chase behaviors in a more controlled condition because the virtual task can set the maximum speed and maneuverability of the pursuer and the target equal and can minimize the influence of their fatigues.

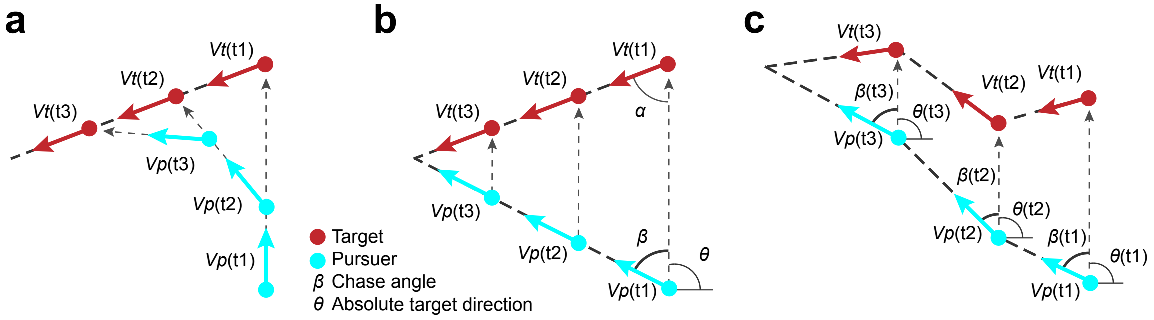

Figure 2-1 Illustrations of navigational strategies

(a) Pursuit of a target moving in a straight line. The target (red disc) moves at a constant velocity and the pursuer (blue disc) moves at a constant speed. The chase angle during the pursuit is always 0 if there is no visuo-motor delay. (b) Interception of a target moving in a straight line. When the target moves at a constant velocity and the pursuer moves at a constant speed, this strategy yields the shortest interception path and maintains a constant absolute target direction during the pursuit. (c) Interception of an erratically moving target. The target moves erratically, changing both speed and direction. The trajectory of an erratically moving target can be broken into short linear segments, and the pursuer moves along the local shortest interception path in each segment.

2.2 Methods

2.2.1 Participant

There were, respectively, twelve male participants who exercised regularly (mean age ± SD = 21.1 ± 2.7 years in the first experiment (real space) and 26.4 ± 3.3 years in the second experiment (virtual space)) in the experiments. All participants were right-handed, had normal or corrected-to-normal vision, and were neurologically healthy. The study was conducted in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the University of Tokyo of Arts and Sciences. Informed consent was received from each participant before the experiments. In the first experiment, participants were divided into two groups of six players and, in the second experiment, participants were divided into six pairs. In both experiments, each member of each group/pair played the roles of both attacker (evader) and defender (pursuer) in turn.

2.2.2 Experimental design

Experiment 1

I conducted the chase-and-escape task in an outdoor field (Figure 2-2). The dimensions of the field were 11 m × 11 m (width × length). The start position of the attacker was the middle of one side of the field, and that of the defender was the center of the field. The objective of the attacker was to move past the defender and reach the end line (yellow line), which was on the other side of the field behind the defender. The objective of the defender was to catch the attacker without the attacker reaching the end line. I regarded a "catch" as a situation in which the defender touched the attacker with both hands. If the attacker left the bounds of the field, the trial was deemed a defensive success. The experimental task began with the start cue. No additional instruction was provided to participants, such as a time limit. After a warm-up session, 30 formal trials were conducted in each group, and thus a total of 60 formal trials were conducted in the first experiment. In each group, a round-robin tournament with six participants was performed. As a result, each participant played the attacker and defender in five trials against different opponents, respectively. The participants were pseudo-randomly assigned to individual trials such that the same participant was not assigned to successive trials.

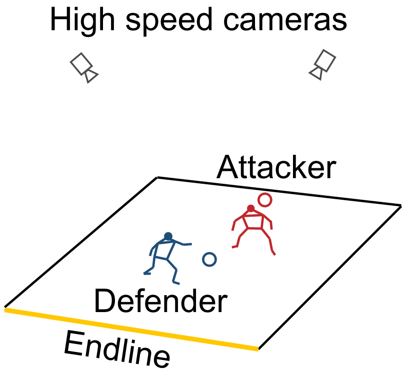

Figure 2-2 Experimental setup of real chase-and-escape task

The dimensions of the field were 11 m × 11 m (width × length). The attacker (red) started from the middle of the one side of the field (red circle), and the defender (blue) started from the center of the field (blue circle). The attacker was required to move past the defender and reach the end line (yellow line). The defender was required to catch the attacker or drive the attacker off of the field.

Experiment 2

I conducted the chase-and-escape task in an indoor room (Figure 2-3). Participants were seated in chairs and manipulated the joystick of a controller (Xbox One) to control a player on a screen. The participants were seated at a viewing distance of approximately 50 cm from the screen. A partition prevented direct viewing of the other player's hands. A red disk (filled circle) onscreen represented an attacker and a blue disk represented a defender. The dimensions of a field were 20 cm × 20 cm (width × height), and the diameter of each disk was 1.0 cm. The start location of the attacker (red disk) was the upper middle of the field, and that of the defender (blue disk) was the center of the field. The objectives of the attacker and the defender and the rules were the same as in Experiment 1. I regarded a "catch" as a situation in which the outer edges of the disks were in contact with each other. The velocity of each agent was determined by the degree of inclination of the joystick on the respective controllers. The maximum speeds of the attacker and the defender were set equally (5.5 cm/s). To provide feedback on the result of each trial to the participants, when the attacker reached the end line (a successful attack), a high-pitched beep sounded. Conversely, when the defender caught the attacker, or the attacker left the bounds of the field (a successful defense), a low-pitched beep sounded. The number of successful attacks was indicated at the end of the trials. After a warm-up session, 100 formal trials were conducted in pairs (each participant played the attacker and defender in 50 trials, respectively), and thus total 600 formal trials were conducted in the second experiment. The role of each participant was randomized between pairs.

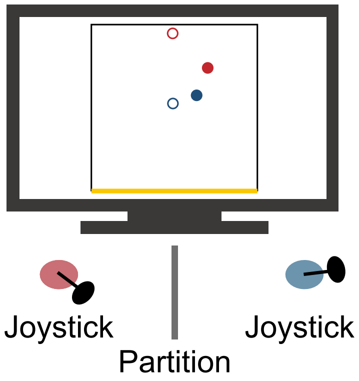

Figure 2-3 Experimental setup of virtual chase-and-escape task

The dimensions of the field were 20 cm × 20 cm (width × height). The attacker (red disc) started from the middle of the one side of the field (red circle), and the defender (blue disc) started from the center of the field (blue circle). The objectives of the attacker and defender were the same as in the real chase-and-escape task.

2.2.3 Data recording

Experiment 1

The task was recorded with two high-speed cameras (Panasonic DMC-FZ1000) operating at 120 Hz above the field. The head center coordinates of the attacker and defender in the

2D image were digitized at 120 Hz using Frame-DIAS (DKH). These data were reconstructed in 3D coordinates using the direct linear transformation (DLT) method via MATLAB (MathWorks). The global coordinate system was defined by *X*, *Y*, and *Z* axes with the origin, which was the middle of the sideline of the filed (near the attacker's initial position). The *X* axis was defined as the lateral direction of the field, the *Y* axis was defined as the longitudinal direction, and the *Z* axis was defined as the vertical direction. To apply the DLT method, eight control points were positioned at the corners of the field on the ground and at a height of 1.6 m, respectively. The height of 1.6 m was determined as almost the same height as the players' head positions during the task. The mean errors of reconstructing the six points in an accuracy test were 2.7, 2.4, and 2.8 cm, for the *X*, *Y*, and *Z* coordinates, respectively. In analysis, I used the *X* and *Y* coordinates, and the coordinates were smoothed by applying a bidirectional fourth-order Butterworth low-pass filter to prevent artifacts. The cut-off frequency for the *X* and *Y* coordinates was 6 Hz (Winter, 2009).

Experiment 2

The task was conducted by using a computer running Psychtoolbox 3.0 software. The stimuli were presented on a 27-inch monitor (ASUS SWIFT PG278Q) at 120 Hz. The central position of each disk onscreen during the trials was recorded at 120 Hz. The global coordinate system was defined by *X* and *Y* with the origin, which was the top left on the screen. The *X* axis was defined as the lateral direction of the field, and the *Y* axis was defined as the longitudinal direction.

2.2.4 Data analysis

All data analysis was performed in MATLAB (MathWorks). Absolute target direction θ

was defined as the angle between a vector that points from the position of pursuer (defender) to that of the target (attacker) and the X axis (see Figure 2-1). I analyzed only the positional data collected while the absolute target direction was in the range of 0 to180 degrees to exclude situations in which the defender had given up trying to catch the attacker. Heading angle was defined as the angle between the velocity vector of defender and the X axis. Chase angle β was defined by the heading angle minus the absolute target direction.

2.2.4.1 Model simulation

To compare the model fit, the chase angle β of each model was calculated in each frame. The residual was defined as an absolute value of the minor angle between the observed and predicted chase angles. The mean residual was calculated for each trial. In comparing the models, I assumed that the speeds of the attacker and defender were always equal because the observed movement speeds of the attacker and defender were approximately 1 to 1 (see Figure S2-1). Taking visuo-motor delay into account, I assumed the pursuer (defender) at time i could use the target's (attacker's) velocity at time $i - \tau$. Whereas, I assumed the target's velocity at time i was available for the pursuer by the short-term extrapolation in which positions of the target at time i were extrapolated by positions and velocities of the target at time $i - \tau$. The τ was estimated as a value minimizing mean residuals within the range of 0 to 1 second (time step was 8.3 ms) in each model. In this case, the chase angle of each model was calculated only in the situations where i was greater than τ, and the other situation was excluded from the analysis. I examined three models: classical pursuit, time-optimal, and parallel navigation models.

Classical pursuit model

The classical pursuit model simulation was given by

$$\beta_i = \theta_{i-\tau} - \theta_i, \tag{1}$$

where θ is the absolute target direction. That is, the chase angle is zero if there is no visuo-motor delay.

Time-optimal model

The time-optimal model simulation was given by

$$\beta_i = \sin^{-1}\left(\frac{\left|\boldsymbol{v}_{t_{i-\tau}}\right| \sin\alpha_i}{\left|\boldsymbol{v}_{p_i}\right|}\right), \tag{2}$$

where $\boldsymbol{v}_t$ and $\boldsymbol{v}_p$ are the velocity vector of the target and pursuer, respectively, and α is the angle between the velocity vector of the target and a vector that points from the target to the pursuer. When $\left|\boldsymbol{v}_p\right| \geq |\boldsymbol{v}_t| \sin\alpha$, there are two solutions to Equation 2, only one of which decreases the distance between the pursuer and the target. Thus, I used the solution that decreases the distance between them as a value of the time-optimal model.

Parallel navigation model

The parallel navigation model simulation was given by

$$\beta_i = \underset{\beta'_i}{\arg\min}\left(\left|\theta_0 - \hat{\theta}_{i+1}\right|\right), \tag{3}$$

where θ_0 and $\hat{\theta}_{i+1}$ are the absolute target direction at time zero (90 degrees) and the estimated absolute target direction at next time step, respectively. The estimated absolute target direction at next time step was estimated by θ_i, $\boldsymbol{v}_{t_{i-\tau}}$, and β'_i. In each frame, the chase angle, minimizes the difference between the absolute target direction at time 0 and that at time *i*+1, was searched from -180 to 180 degrees in 1 degree steps. If there are two solutions, I used the solution that decreases the distance between them as a value of the parallel navigation model.

2.2.4.2 Phase division

To investigate whether the model fit differed between phases, I divided the trials into a turning phase and a straight phase, and I calculated the residuals in each phase. The turning phase was defined as 250 ms before and after the timing at which the predicted chase angle crosses zero. The chase angle crosses zero means that defender's turn (i.e., left to right or right to left) relative to the attacker's position. When the situation in which the turning phases overlap, such as an attacker conducted two consecutive turns in a short interval, the turning phases were connected. The straight phase was defined as any other time during the trial.

2.2.4.3 Response time

To examine the relationship between estimated visuo-motor delay and response time, I computed response times. The response time was defined as the time between a time of direction reversal of the attacker and that of the defender. The time of direction reversal was defined as the time when the velocity in the X direction crossed zero. I distinguished between positive and negative X velocities. I limited the range of response times from 0 ms to 500 ms and removed any response times longer than 500 ms from the analyses to exclude responses in which the defender had given up trying to catch the attacker. For both experiments, more than 90% of the responses passed this criterion.

2.2.5 Statistical analysis

To compare the mean residuals among the three models, one-way repeated measures ANOVA was used. In the ANOVA, I tested sphericities using Mauchly's test, and, if the sphericity assumption was violated, I adjusted the degree of freedom using Greenhouse-Geisser correction ε. A paired *t*-test or Wilcoxon signed-rank test with Bonferroni correction was used to compare the variables within the factor where a significant effect in ANOVA. To test the relationship between the observed chase angle and the predicted chase angle in the time-optimal model, I used circular statistics instead of Pearson's product-moment correlation analysis because the values are both circular (Berens, 2009). The correlation coefficients were compared to 0 after Fischer *Z*-transformation using Student *t*-test. For comparison of the mean residuals between phases (straight and turning), I used Wilcoxon signed-rank test. For comparison of proportions of successful defense between the experiments (real space and virtual space) and of the variables between the outcomes (successful defense and unsuccessful defense), I used unpaired *t*-test if the normality assumption was accepted by Lilliefors test. If rejected, Mann-Whitney *U* test was used. The effect size was estimated using Cohen's *d* for *t*-test, eta-squared value (η^2) for ANOVA, and *r* for Wilcoxon signed-rank test and for Mann-Whitney *U* test. The statistical significance level was set at $p < 0.05$ and was set at $p < 0.0167$ in the post hoc multiple comparison. Statistical analyses were performed using the MATLAB Statistical Toolbox (MathWorks), the R version 3.5.1 (The R Foundation).

2.3 Results

Experiment 1 and 2

First, I illustrate typical examples of trajectories for the players in the trials of successful defense in the real and the virtual spaces, respectively (Figures 2-4a and b). In this task, the attacker and defender approached at the beginning of the trial, and afterward the distance between two was maintained at an approximately constant. In these trials, although the attacker made a change in direction from side to side to pass the defender, the defender eventually succeeded in catching the attacker (right side in Figure 2-4a and left side in Figure 2-4b). The mean duration of the trial was 6.5 ± 2.7 seconds in real space and 4.9 ± 1.8 seconds in virtual space, and there was no significant difference between spaces (t_{22} = 1.76, p = 0.093, d = 0.72).

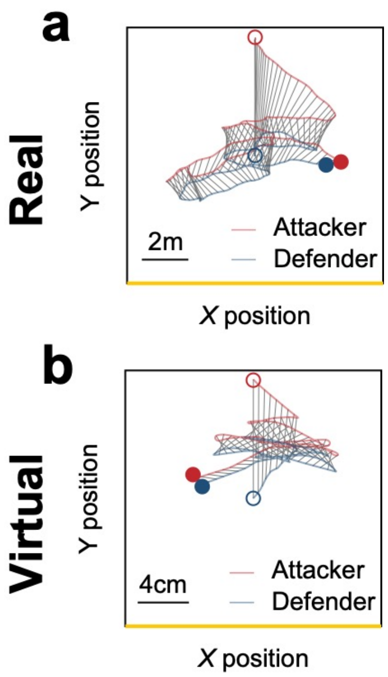

Figure 2-4 Trajectories of the players in typical trial

(a, b) Trajectories of the players in a typical trial (a) in the real space and (b) in the virtual space. The defender caught the attacker (a) in the middle right of the field in the real space and (b) in the middle left of the field in the virtual space. The gray lines connected the positions of the attacker and defender in 100 ms steps.

Then, I focused on the movement direction of pursuer to examine its navigational strategy for intercepting a target. Figures 2-5a and b show the time series of observed chase angle and the predicted chase angle by the models proposed in human interception studies. The classical pursuit model always predicted the chase angle as zero degrees (i.e., direct movement toward the attacker at each moment), and it indicated that the predicted chase angle did not match the observed chase angle (upper). The prediction of time-optimal model was approximately consistent with the observation during the trial (middle). The parallel navigation model predicted the chase angle as -90 or 90 degrees in most time of the trial to correct the deviations of an absolute target angle from the beginning of the trial, and it indicated that the prediction did not match the observation (lower).

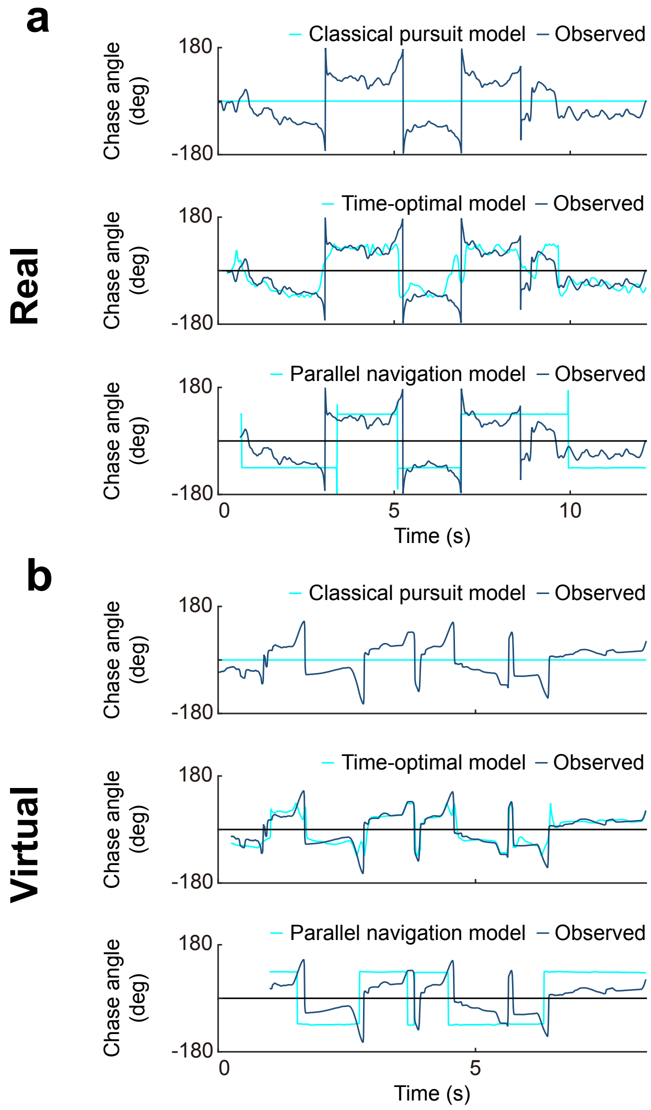

Figure 2-5 Model comparison of the time series data in typical trial

(a, b) Time series of observed and predicted chase angles by the classical pursuit model (upper), the time- optimal model (middle), and the parallel navigation model (lower) during the trial (a) in the real space and (b) in the virtual space. In these model simulations, I used visuo-motor delays estimated in each model (see Figure 2-6).

Figure 2-6 shows the quantitative comparison among the three models. In each model, I calculated mean residuals at each delay from 0 to 1 second (time step was 8.3 ms) to take visuo-motor delay of the pursuer into account. The minimum residual was taken as the representative value of each model. A one-way repeated measures ANOVA revealed a main effect and post hoc analyses revealed that the time-optimal model was significantly better fit than the others (Figure 2-7; real space: $F_{1.17,12.9} = 21.1$, $p < 0.001$, $\eta^2 = 0.54$, $ps < 0.05$, $ds > 1.1$; virtual space: $F_{1.11,12.24} = 61.9$, $p < 0.001$, $\eta^2 = 0.81$, $ps < 0.01$, $ds > 2.1$).

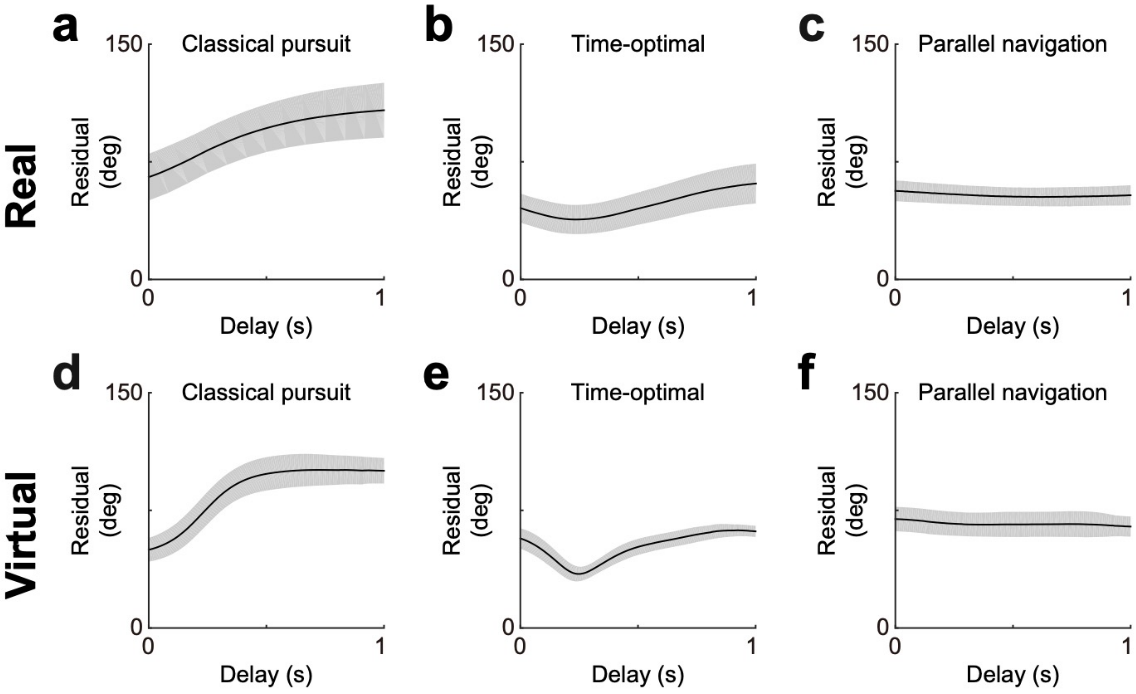

Figure 2-6 Model comparison in each delay

(a-c) The mean residuals of (a) the classical pursuit model, (b) the time-optimal model, and (c) the parallel navigation model in each delay in the real space. (d-f) The mean residuals of the (d) the classical pursuit model, (e) the time-optimal model, and (f) the parallel navigation model in each delay in the virtual space. CP, TO, and PN refer to the classical pursuit, the time-optimal, and the parallel navigation models, respectively. The minimum residual was taken as the representative value of each model.

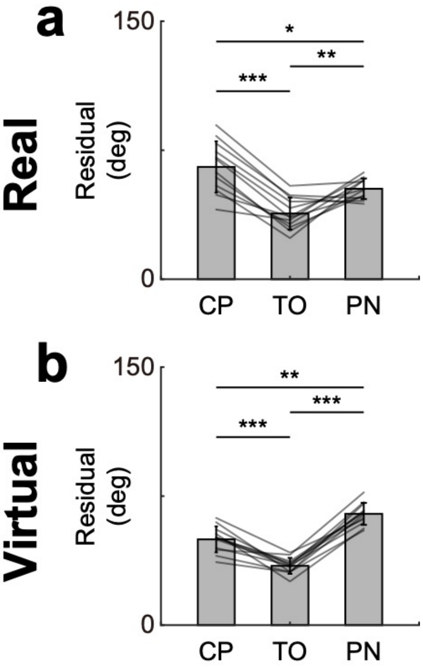

Figure 2-7 Model comparison

(a, b) Comparison of the representative mean residuals among the models (a) in the real space and (b) in the virtual space. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

To visualize the association between the observed chase angles and predicted chase angles by time-optimal model, I show color-coded 2D histograms between those (Figure 2-8 and Figure S2-2). There were strong positive correlations in both spaces (real space: t_{11} = 13.0, $p < 0.001$, ρ = 0.76 ± 0.16; virtual space: t_{11} = 23.4, $p < 0.001$, ρ = 0.76 ± 0.03). The 2D histograms indicated that the observed chase angle was approximately consistent with the predicted chase angle (i.e., the distributions were around on $X = Y$), whereas there were some deviations.

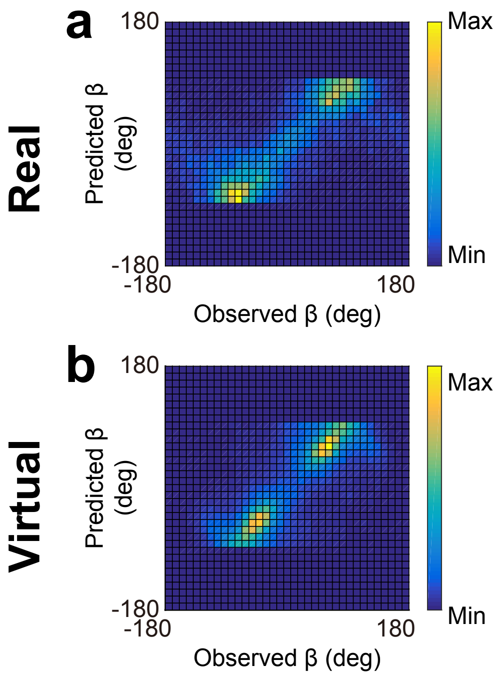

Figure 2-8 Fitness of time-optimal model

(a) 2D histograms of the chase angles between observation and time-optimal model prediction of all data in real space (60 trials). The width of each cell was set to 10 degrees. There was positive correlation ($\rho = 0.76 \pm 0.16$). (b) 2D histograms of the chase angles of all data in virtual space (600 trials). There was positive correlation ($\rho = 0.76 \pm 0.03$).

Then, I examined in more detail the deviation between the observed chase angles and predicted chase angles by the time optimal model. Figure 2-9 shows the difference of mean residuals with the time-optimal model in straight phase and in turning phase. The gray parts in Figure 2-9 show the turning phase, and the other white parts show the straight phase.

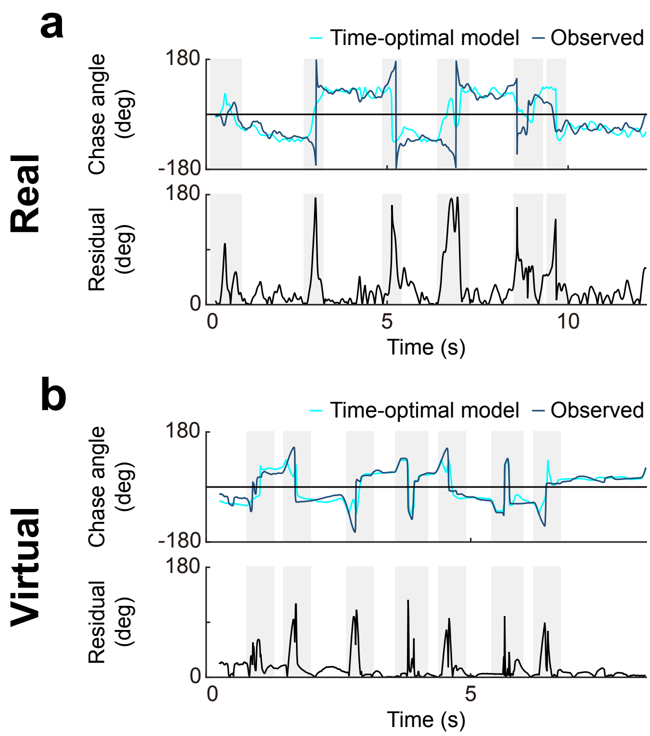

Figure 2-9 Deviation from time-optimal model in typical trial

(a, b) Time series of the chase angles and residuals during the typical trial in each phase (a) in the real space and (b) in the virtual space. The gray parts indicate the turning phase, and the white parts indicate the straight phase.

The deviation from the time-optimal model in the turning phase was significantly greater than that in the straight phase in both spaces (Figures 2-10a and c; real space: $W = 78$, $p < 0.01$, $r = 0.62$; virtual space: $W = 78$, $p < 0.01$, $r = 0.62$). In addition, I found that the remarkable deviations from the time-optimal model in which the absolute value of observed chase angle exceeds 90 degrees were largely in the turning phase (see Figure S2-3). The histogram of the response time of the defender (pursuer) for sudden turn of the attacker (evader) showed that the response times were distributed around 250 ms in both spaces (Figures 2-10b and d).

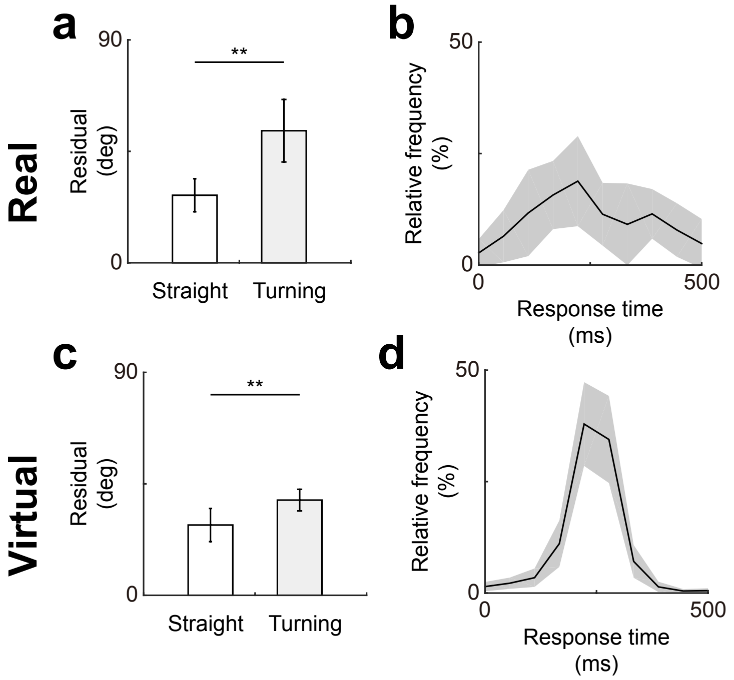

Figure 2-10 Deviation from time-optimal model

(a, c) Comparison of the residuals in each phase across participants (a) in the real space and (c) in the virtual space. (b, d) Histogram of the response time of the defender (pursuer) for a sudden turning direction of the attacker (evader) (b) in real space and (d) in virtual space. The width of each bin was set to 50 ms. $**p < 0.01$.

Finally, I examined the relationship between the model fit and the trial outcome. In this analysis, I focused the residual and the visuo-motor delay because the defender completely following the time-optimal model without delay is theoretically unbeatable. Figure 2-11 shows the comparison of mean residuals with the time-optimal model in successful defense and unsuccessful defense. The proportion of successful defense was 0.70 ± 0.20 (42 out of 60 trials in total) in the real space and 0.78 ± 0.20 (468 out of 600 trials in total) in the virtual space (Figures 2-11a and e), and there was no significant difference between spaces ($t_{22}= 0.99, p > 0.05, d = 0.40$). The mean residuals at the best fit τ were not significantly different in the real space (Figure 2-11c; $U = 3.7\times10^2$, $p > 0.05$, $r = 0.03$), whereas the mean residual in successful defense was smaller than that in unsuccessful defense in the virtual space (Figure 2-11g; $U = 2.2\times10^4$, $p < 0.001$, $r = 0.15$). There was no significant difference between the estimated visuo-motor delay in both spaces (Figures 2-11d and h; real space; $t_{58} = 0.76$, $p > 0.05$, $d = 0.21$; virtual space; $U = 2.9\times10^4$, $p > 0.05$, $r = 0.04$).

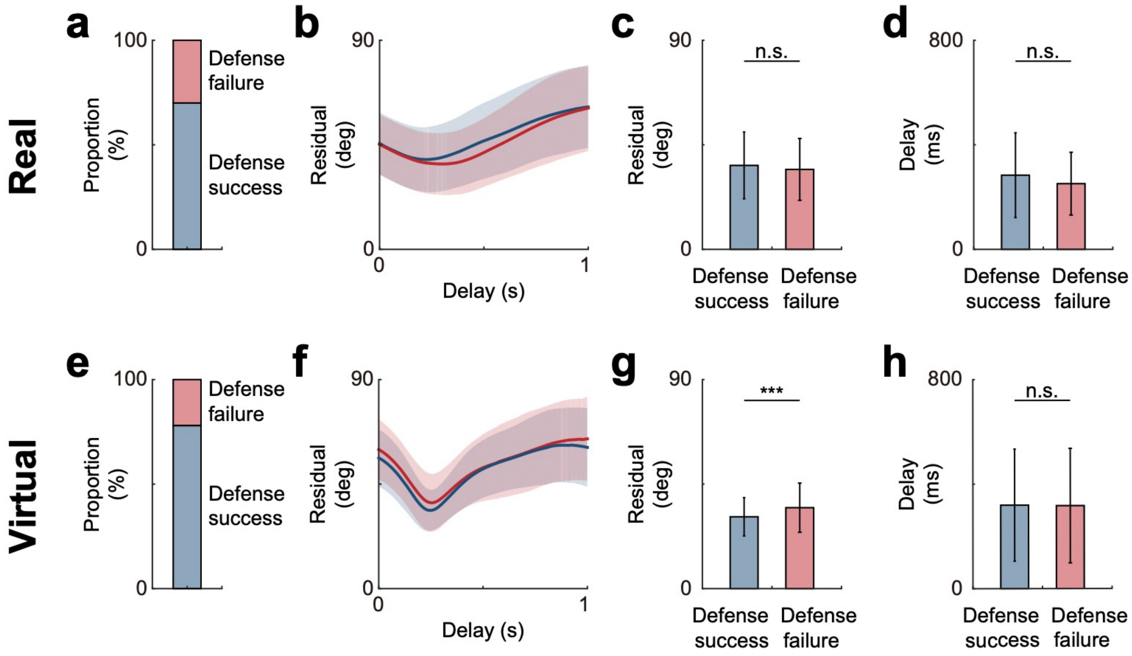

Figure 2-11 Comparison between successful and unsuccessful defense

(a, e) The proportion of successful and unsuccessful defense (a) in the real space and (e) in the virtual space. (b, f) The mean residuals of the time-optimal model in each delay in successful defense (blue line) and unsuccessful defense (red line) (b) in the real space and (f) in the virtual space. (c, g) Comparison of the representative mean residuals (c) in the real space and (g) in the virtual space. (d, h) Comparison of the estimated visuo-motor delay, which is the delay minimizing the mean residuals (d) in the real space and (h) in the virtual space. ***$p < 0.001$.

2.4 Discussion

The present study explored the human navigational strategy for intercepting a moving target in chase-and-escape interactions. The results demonstrated that the pursuer's chase angle was more statistically consistent with the time-optimal model than the other models and there were strong positive correlations between the observation and time-optimal model prediction in both experiments, namely the chase-and-escape tasks in real space and virtual space. In addition, these revealed that the deviation from the time-optimal model was larger in the turning phase than in the straight phase.

The time-optimal model showed a better fit with human interception behaviors in the chase-and-escape interaction than the other models. One possible strategy was classical pursuit, in which a pursuer moves directly toward the target. Although this strategy allows the pursuer to catch the target if the purser moves faster than the target, it has been considered inefficient due to a curved path in some conditions where a target moves. Thus, in chase-and-escape interactions, this strategy could be less suitable than the other strategies. In fact, we confirmed that the classical pursuit model was less consistent with the observed pursuer's behavior in the present study. Another possible strategy was parallel navigation, in which a pursuer selects an interception path such that the target direction in an absolute coordinate system is kept constant. In the present study, the pursuer moves so as to maintain the absolute target direction θ at 90 degrees, that is the pursuer nulls $|90 - \theta|$. In our task, which is similar to one-on-one situations in ball sports, the pursuer (defender) is theoretically unbeatable as long as the direction of the target (attacker) is maintained at the original angle. Thus, I considered that this strategy may be used by the pursuer. However, our results showed that the parallel navigation model was less consistent with the observed behaviors. One reason that this strategy was not used may be due to the escape behavior of the attacker. The absolute target direction could be also used as information for collision avoidance as well as information for interception (Cutting, Vishton, & Braren, 1995). In other words, to avoid a moving object, it is necessary to move so that the absolute target direction (or pursuer direction as seen from the target) is not constant; if the absolute target direction is increasing (to 180 degrees), the attacker will pass the defender from the left side, and if it is decreasing (to 0 degrees), the attacker will pass the defender from the right side. For that reason, the attacker would move so as to prevent the absolute target direction maintaining at a constant, and thus the parallel navigation strategy might be less suitable for the present chase-and-escape tasks. Compared to these strategies, the time-optimal strategy may be useful in the chase-and-escape task, where spatiotemporal constraints are severe and the movement trajectory and the final destination of the target are not predetermined, because it yields the local time-optimal (shortest) path to intercept the target. Interestingly, behaviors consistent with strategies similar to the time-optimal strategy in this study have been observed in the studies on hand interception (Dessing et al., 2002; Dessing, Peper, Bullock, & Beek, 2005; Reid & Dessing, 2018; von Hofsten, 1983). For example, the RRVITE model well explained the hand interception (Dessing et al., 2002). Also, the bidirectional model of attacker and defender was proposed in the one-on-one study and well reproduced the interactive behaviors of two (Fujii, Isaka, et al., 2015). Thus, although three models were compared in this study, further examinations by integrating many other models related to the interception of moving target would be necessary for a better understanding of human interception behaviors.

When the visuo-motor delay of the pursuer was considered, the fit with the time-optimal model was improved. It has been shown that a visuo-motor delay, which is the latency from visual input to motor output, is inevitable in animals and is about 200 milliseconds in human interception (Franklin & Wolpert, 2011; Smeets & Brenner, 1994). In fact, previous studies involving non-humans have shown that pursuit and interception behaviors are more accurately explained by assuming sensorimotor delay (Gilbert, 1997; Haselsteiner et al., 2014). Similarly, the fit of human interception behavior with the time-optimal model was improved by assuming the visuo-motor delay of the pursuer. The estimated visuo-motor delay was 250 ms in both experiments, and this delay time is considered as the response time of the pursuer. In the time-optimal model simulation, a single visuo-motor delay τ was used, but there was variation in actual responses. This difference could have contributed to increase the deviation from the model in the turning phase. In addition, the distributions of actual response time were somewhat different between experiments (see Figures 2-10b and d). It has been shown that defenders try to predict the timing of turning using kinematic information on the attacker's body parts (Brault et al., 2012). On the other hand, attackers perform feint (deceptive) movements in order to exploit such predictions of the defender (Brault et al., 2010). As a result, the response time become short when the defender's prediction works well, and that become long when the attacker's feint works well. Our results that the distribution of response time in real space is more spread than that in virtual space might be related to the presence or absence of such body kinematics information.

Previous studies involving many animals have shown that interception behaviors in chase-and-escape interactions, namely hunting, can be explained by the time-optimal model. In the present study, I used the chase-and-escape task as seen in ball sports, which is somewhat different from the chase-and-escape interactions in the natural world where an evader can run away in free directions. Thus, there was also the possibility that the defender uses a task specific strategy (e.g., the defender waits for the attacker to come closer). In general, most studies have assumed that the defenders tend to be passive because they respond to the attackers' maneuvers (Brault et al., 2012; Jackson et al., 2006; Murphy, Jackson, & Williams, 2018; Wright & Jackson, 2014). For example, the previous study focusing on defenders in rugby used the experimental paradigm that the defenders catch the attackers coming toward them by side-stepping (Brault et al., 2012). On the other hand, our results showed that the defender basically moved along the local time-optimal path, and it indicates that the chase angle was 90 degrees or less in absolute at many times during the pursuit. In other words, the defender tried to approach the target, and it suggests that the defender may behave actively (like predators) in some situations.

Our two experiments were different in several aspects. One was the viewpoint, that is, egocentric view in the real space and bird's eye view in the virtual space. Although this difference might affect interception behavior, the results of the present study had common tendencies in both experiments, and it suggests that the effect was minor. Many studies have shown that the target direction and its derivatives would be important visual information for intercepting a moving target (Chapman, 1968; McBeath et al., 1995; McLeod et al., 2003; Wang et al., 2015). In both of two experiments, this visual information was available and that may explain why the interception behaviors in both experiments were similar.

2.5 Summary

In summary, I conducted two chase-and-escape tasks, and the results showed that the pursuer's behavior was well reproduced by the time-optimal model in both experiments. These results suggest that humans use the time-optimal strategy for intercepting a target in chase-and-escape interactions.

Chapter 3 Study 2

Spatiotemporal characteristics of an attacker’s strategy to pass a defender effectively in chase and escape interactions

This study has been published as:

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3.1 Introduction

Our decisions are often made in competitive interactions with others. In such situations, agents must achieve their own purpose in the interaction despite the conflicting purposes of other agents. A typical example of a competitive interaction is chase-and-escape behavior. Chase-and-escape interactions are ubiquitous in nature (predator-prey), and similarly feature in many sports, such as football, rugby, and basketball (defender-attacker) (Ghose et al., 2006; Lee, Georgopoulos, Clark, Craig, & Port, 2001; Wei, Justh, & Krishnaprasad, 2009). In these interactions, the agent's decisions on when and where to move are essential for survival and success (Domenici et al., 2011a; Wilson et al., 2015). Thus, it is important to consider how the agents make such decisions in these competitive interactions.

Decisions regarding direction changes are important in chase-and-escape interactions. Previous studies on many animals, ranging from dragonflies (Mischiati et al., 2014; Olberg et al., 2000; Olberg, 2012), to fish (Lanchester & Mark, 1975) and dogs (Shaffer, Krauchunas, Eddy, & McBeath, 2004b), to humans (Fajen & Warren, 2004, 2007; Wang et al., 2015), have shown that they commonly use a strategy called constant bearing to intercept a moving target, such as prey, a frisbee, or a flying ball. When the pursuer’s speed is equal to or faster than that of the evader, this interception strategy is theoretically unbeatable without a sensorimotor delay (Nahin, 2012). This time delay, which is the latency from sensory input to motor output, is inevitable in animals and can be several hundred milliseconds in humans (Franklin & Wolpert, 2011). Consequently, from the perspective of the evader, lengthening (or at least not shortening) the visuo-motor delay (response time) of the pursuer should lead to a successful escape (Fujii, Isaka, et al., 2015).

One possible evader strategy is to increase the unpredictability of its actions. In several studies on interceptive behaviors in severe time constraints, such as in cricket, tennis, and handball, it has been reported that a pursuer (receiver or goalkeeper) anticipates the opponent's movement using prior knowledge (experience), which is a probability distribution accumulated by long periods of observation (Abernethy, Gill, Parks, & Packer, 2001; Farrow & Reid, 2012; Mann, Schaefers, & Cañal-Bruland, 2014). For example, in a handball penalty shot, when there is a probability bias in an opponent's shot direction, the goalkeeper is more likely to respond in that direction than to respond as if the opponent's shot is equally likely to occur in either direction (Mann et al., 2014). These studies suggested that the pursuer should use the situational (event) probability information to anticipate the opponent's movement in interceptive behaviors. Given that the defender predicts the movement of the attacker to compensate for its own visuo-motor delay, it should be useful for the attacker to increase the unpredictability of its own movements against the defender.

Another possible strategy of the evader is to increase efficiency. In the psychological refractory period paradigm, in which two stimuli are presented in close succession, it has been shown that the response time to the second stimulus increases if the time between stimuli is short (400 ms or less) (Pashler, 1994; Smith, 1967; Telford, 1931; Welford, 1952; Zylberberg, Ouellette, Sigman, & Roelfsema, 2012). From the stimulus-response viewpoint, if the attacker's two consecutive movements direction changes, such as moving right to left to right, the defender's response to the second direction change could be delayed. Given that the defender's response to the attacker's direction change is delayed in such a situation, the attacker could iterate effective direction changes.

To address these possibilities, we examined probability distributions regarding the direction change of the attacker and the response time of the defender. In this study, we conducted a computer-based one-on-one task, which eliminates kinematic information to focus on the situational probability information. Our results suggest that the direction changes of the attacker have effective spatiotemporal characteristics that combine both of the above two possibilities to pass the defender.

3.2 Methods

3.2.1 Participants

Twelve participants (mean age ± SD = 24.9 ± 2.3 years) who exercised regularly participated in the experiment. All participants were right-handed, had normal or corrected-to-normal vision, and neurologically healthy. The study was conducted in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the University of Tokyo of Arts and Sciences. Informed consent was received from each participant before the experiments. In both experiments, participants were recruited in pairs, and each member of each pair took on the roles of both attacker (evader) and defender (pursuer) in turn.

3.2.2 Experimental apparatus

Participants were seated in chairs and manipulated the joystick of a controller (Xbox One) to control a disk (filled circle) on the screen. The central position of the disk was recorded on a computer (Sony SVF152C16N) running Psychtoolbox 3.0 software at a frequency of 60 frames/s and a resolution of 1366 × 768 pixels. The stimuli were presented in a lit room on a 15.5 in (34.3 × 19.3 cm) screen. The participants were seated at a viewing distance of 50 cm. A partition prevented direct viewing of the other player's hands.

3.2.3 Experimental design

Participants controlled either a red disk representing an attacker or a blue disk representing a defender on the screen (Figure 3-1). The dimensions of the onscreen court were 33.1 cm × 16.6 cm (width × height). The diameter of each disk was 1.0 cm. The start location of the attacker (red disk) was the upper middle, and that of the defender (blue disk) was the center of the court. The objective of the attacker was to move past the defender and reach the end line, which was on the lower side of the court (a yellow line) behind the defender. The objective of the defender was to catch the attacker without the attacker reaching the end line. I regarded a “catch” as a situation in which the outer edges of the disks were in contact. If the attacker left the bounds of the court, the trial was deemed a defensive success. The velocity of each agent was determined by the degree of inclination of the joystick on the respective controllers. The maximum speeds of the attacker and the defender were set equally. The experimental task began with a start cue. No additional instructions, such as a time limit, were given to the participants. To provide feedback on the result of each trial to the participants, when the attacker reached the end line (a successful attack), a high-pitched beep was played. Conversely, when the defender caught the attacker, or the attacker left the bounds of the court (a successful defense), a low-pitched beep sounded. The number of successful attacks was indicated at the end of each block; blocks consisted of 30 trials.

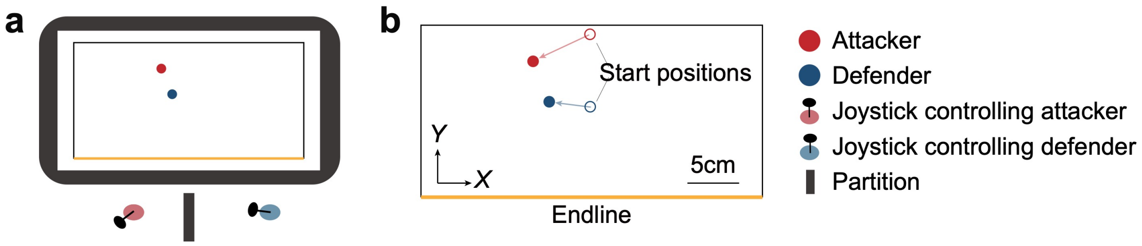

Figure 3-1 Experimental setup

(a) Illustration of experimental setup. Participants controlled either a red disk representing an attacker or a blue disk representing a defender on the screen using a joystick. A partition prevented direct viewing of the other participant's hands. (b) Experimental task. The start location of the attacker was the upper middle (red circle) and that of the defender was the center (blue circle) of the court. The objective of the attacker was to move past the defender and reach the end line (yellow). The objective of the defender was to catch the attacker (contact the outer edges of the disks). If the attacker left the bounds of the court, the trial was deemed a defensive success. The velocity of each agent was determined by the degree of inclination of the joystick on the respective controllers.

3.2.4 Experimental conditions

I used two experimental conditions in this study (slow and fast) to examine the speed dependency of agent decision making. In previous studies, it has been reported that the required movement speed (time constraint) may affect the agent's interception strategies (reactive or predictive) (Farrow & Reid, 2012; Wong & Haith, 2017). In a one-on-one sports situation, as the agents' movement speeds increase, it becomes more difficult for the defender to intercept the attacker (Araújo et al., 2014). Thus, to test the possibility that changes in the defender's strategy (and changes in the attacker's strategy corresponding to the defender's strategy) depended on the agents' movement speeds, I set two speed conditions. The slow condition was set so that the defender could easily intercept the attacker, and the fast condition was set so that the possibility of interception (successful defense) or penetration (successful attack) of the two agents was balanced. The minimum speed of the agents (both attacker and defender) was 0 cm/s in both conditions, and the maximum speed of the agents was 3 cm/s in the slow condition and 4.5 cm/s in the fast condition. There were 40 warm-up trials and 240 experimental trials per pair of participants. The experimental trials were presented in 8 blocks of 30 trials each. For each condition, participants performed 4 blocks (60 trials in each role of attacker and defender; 120 trials total). The role of each participant was randomized between blocks, and the experimental condition was randomized between pairs. The experiment lasted approximately an hour.

3.2.5 Data analysis

All data analysis was performed in MATLAB (MathWorks). I recorded the onscreen *X* and *Y* positions of the attacker and defender during the trial. I analyzed only the positional data collected while the absolute angle between the defender and the attacker was in the range of 0 to180 degrees to exclude situations in which the defender had given up trying to catch the attacker.

3.2.5.1 Direction change

The direction change time was defined as the time when the velocity in the *X* direction crossed zero, and the position at that time was defined as the direction change position.

3.2.5.2 Response time

The response time was defined as the time between the direction change time of the attacker and that of the defender. I distinguished between positive and negative X velocities. I limited the range of response times from 0 ms to 500 ms and removed any response times longer than 500 ms from the analyses to exclude responses in which the defender had given up trying to catch the attacker. The proportion of responses passed this criterion was 0.99 ± 0.01.

3.2.5.3 Frequency

The frequency was defined as the average number of occurrences per second. In other words, the frequency was calculated by dividing the number of direction changes by the time over which they spent.

3.2.5.4 Standard deviation of frequency

The standard deviation (SD) of the frequency was calculated using the frequency value in each X column. In this case, I divided the court into 10 X columns and used the frequency values in the middle 6 columns to exclude the columns containing missing values. Missing values indicated that the attacker did not move to those X columns.

3.2.5.5 Classification of Direction change

In the analysis of the temporal aspect, the direction change was classified into two types depending on the time elapsed from the previous direction change: short-interval direction changes (< 350 ms) and long-interval direction changes (> 350 ms). The boundary between them was 350 ms in both conditions. To determine this boundary, I fitted a mixture model containing a multimodal Gaussian distribution. The number of Gaussian distributions was 4, which was determined using Akaike's Information Criterion. I estimated the parameters of this model using maximum likelihood estimates.

3.2.6 Statistical analysis

To compare the successful attack rates between conditions, I used paired *t*-test due to the normality assumption was accepted by Lilliefors test. To compare the frequency of direction changes of attacker, a two-way repeated measures ANOVA with the factors of speed condition (slow, fast) and X position was used. In this comparison, the X position was divided into 10 columns, and I used the middle 6 columns in the statistical test to remove the columns containing missing values caused by the attacker never changing direction in those columns. To compare the SD of the frequency of direction changes of attacker, a two-way repeated measures ANOVA with the factors of speed condition and X position and with the factors of speed condition and number of trials was used. In this case, the term of "number of trials" indicated the number of cumulative trials, and the comparison was made among 0 to 10, 0 to 20, 0 to 30, 0 to 40, 0 to 50, and 0 to 60 trials. To compare the response time of defender, two-way repeated measures ANOVAs with the factors of speed condition and number of trials was used. In this comparison, the X position was divided into 10 columns, and I use the middle 4 columns in the statistical test to remove columns containing missing values caused by the defender failing to respond to the direction change of the attacker in those columns. In this case, the term of "number of trials" indicated each 10 trial, and the comparison was made among 0 to 10, 11 to 20, 21 to 30, 31 to 40, 41 to 50, and 51 to 60 trials. To compare the response time of defender, a two-way repeated measures ANOVA with the factors of speed condition and the time interval (time from the previous direction change of the attacker) was used. In this case, I removed one participant from the statistical test because the participant included missing values caused by the opponent (attacker) never changing direction during the time interval. In the ANOVAs, Greenhouse-Geisser correction was applied for the violations of sphericity assumption in Mauchly test. Multiple comparisons with Bonferroni correction were applied in the post hoc analysis. To compare the distribution of positions of direction change with the short-interval and that with the long-interval, Kolmogorov–Smirnov test was used. The significance level was set at $p < 0.05$ and adjusted with Bonferroni correction in the multiple comparisons. The effect size was estimated using Cohen's *d* for *t*-test and multiple comparison and eta-squared (η^2) for ANOVA. The achieved power ($1-\beta$) was computed by post hoc power analysis. No statistical methods were used to predetermine sample sizes. All data are reported as mean ± SD across subjects. Statistical analyses were performed using the R version 3.5.1 and G*power version 3.1(Faul, Erdfelder, Lang, & Buchner, 2007).

3.3 Results

The successful attack rates were 14.2 ± 13.2% in the slow condition and 51.8 ± 11.8% in the fast condition ($t_{11} = 7.37, p = 1.4\times10^{-5}, d = 3.02, 1-\beta = 1.0$).

I illustrated the overwriting of the attackers' trajectories from all trials in each condition (Figures 3-2a and i) and the 2D-histogram (i.e., heat map) at each position (Figures 3-2c and k). In this case, the court was divided into the 968 (44 × 22) cells of 30 square pixels each. Then, I plotted the direction change positions of the attackers (Figures 3-2b and j) and the 2D-histogram at each position (Figures 3-2d and i). The frequency of direction changes at each position was almost uniform (Figures 3-2e and m). I focused on the data in the *X* direction and quantified them. Figures 3-2f and n show the time that the attacker spent within each *X* column, and Figures 3-2g and o show the numbers of direction changes. Figures 3-2h and p show the frequency of direction changes. A two-way (condition and *X* position) repeated measures ANOVA revealed a main effect of the condition ($F_{1,11} = 13.29, p = 0.0039, \eta^2 = 0.068, 1-\beta = 0.90$). Notably, however, the main effect of *X* position and the interaction between these factors were not significant ($F_{5,55} = 1.905, p = 0.11, \eta^2 = 0.028, 1-\beta = 0.26$; $F_{5,55} = 0.791, p = 0.56, \eta^2 = 0.0093, 1-\beta = 0.083$).

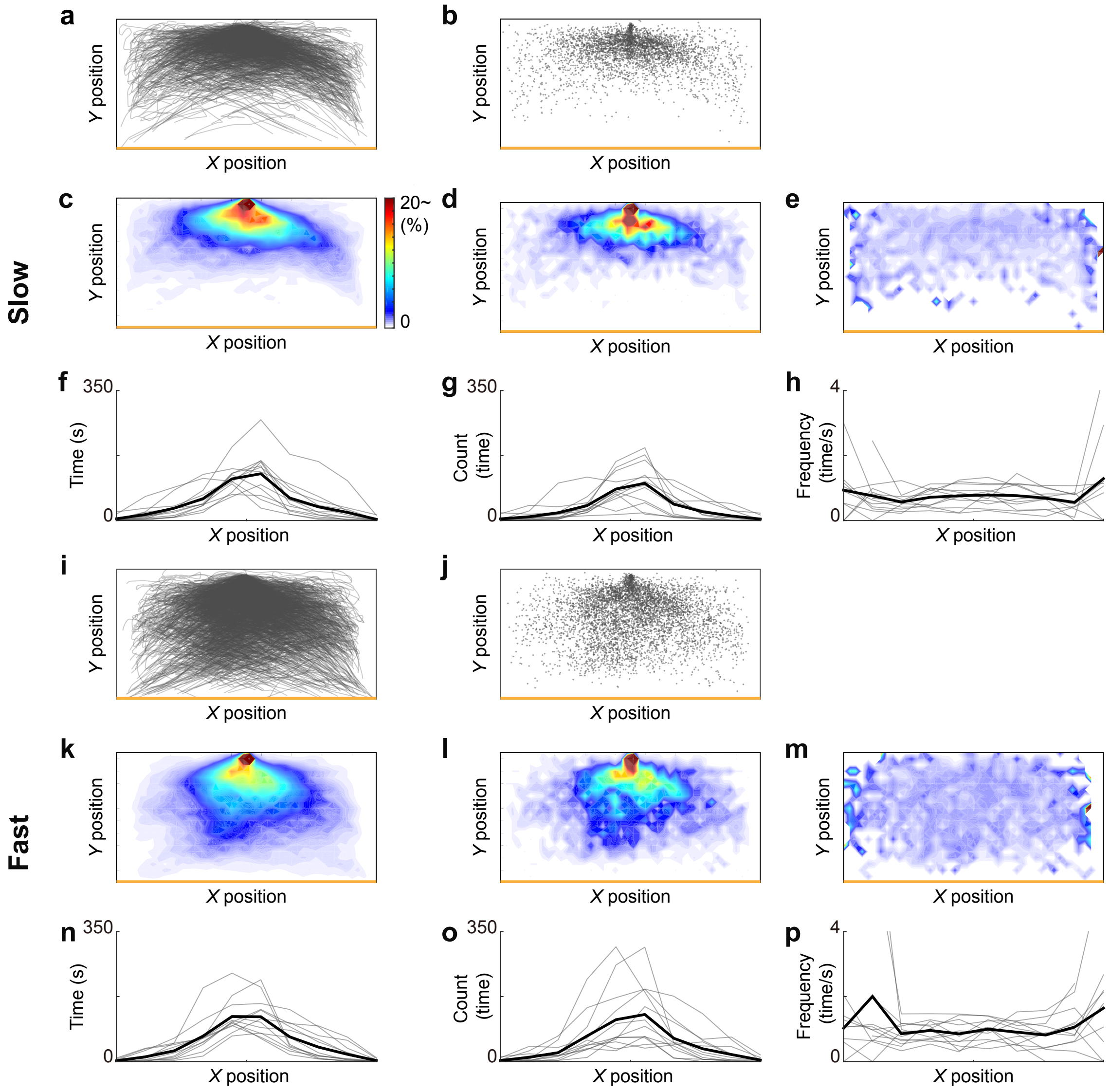

Figure 3-2 Spatial characteristics regarding direction changes

(a–h) Results of the slow condition and (i–p) those of the fast condition. (a, i) Overwriting of the attackers' trajectories from all trials, and (c, k) 2D-histograms at each position. The court was divided into 968 (44 × 22) cells of 30 square pixels each. (f, n) Histograms of attacker time spent in different *X* positions for each participant. The *X* position was divided into 10 columns. (b, j) The direction change points in *X* position of the attackers from all trials, and (d, l) 2D-histograms at each position. (g, o) Histograms of the direction changes in the *X* position of each participant. (e, m) The frequency of direction changes at each position from all trials (e = d/c, m =l/k). (h, p) The frequency of direction changes in *X* position of each participant (h = g/f, p = o/n).

Figures 3-3a and b show typical examples of attacker data for a participant in each condition. Each figure shows the cumulative changes in time spent in the column (left), in the number of direction changes (middle), and in the frequency (right) of the attacker in each *X* column through all trials.

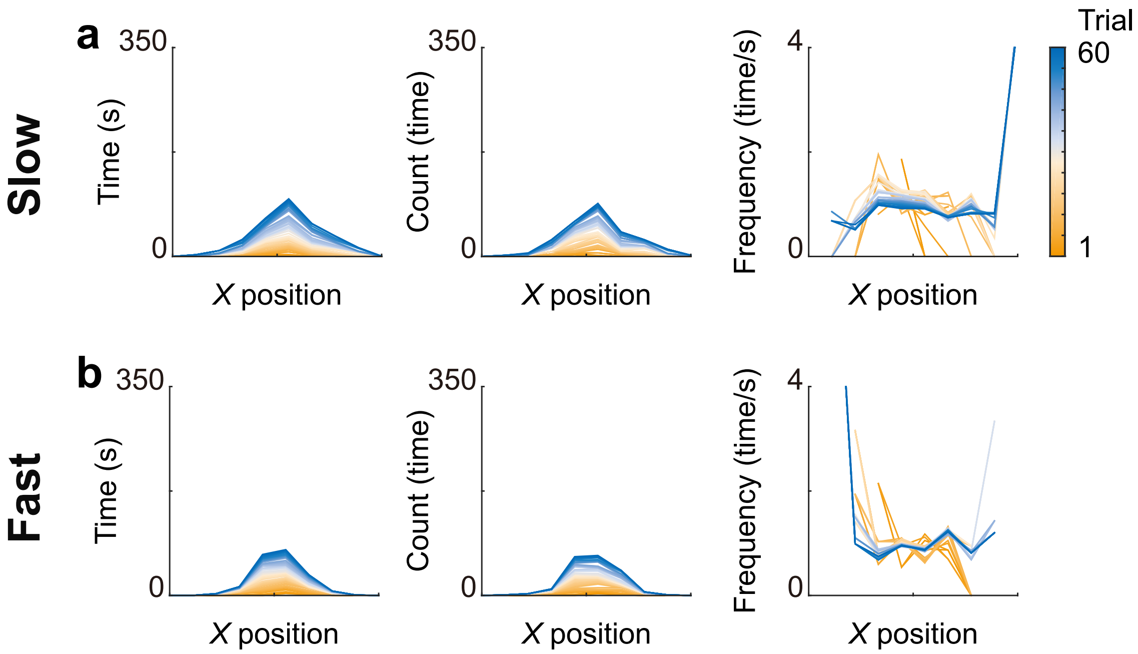

Figure 3-3 Cumulative changes in the frequency in typical attacker

(a, b) Cumulative changes of the frequency regarding the direction changes of typical attacker (a) in the slow condition and (b) in the fast condition. Each color represents the accumulated data up to each trial.

In the SD of the frequency between *X* columns, a two-way (condition and trials) repeated measures ANOVA revealed a main effect of trials (Figure 3-4; $F_{1.97, 21.68} = 11.72$, $p = 4.0\times10^{-4}$, $\eta^2 = 0.21$, $1-\beta = 0.96$). The conditions and the interaction between these factors were not significant ($F_{1, 11} = 1.51$, $p = 0.25$, $\eta^2 = 0.029$, $1-\beta = 0.54$; $F_{2.31, 25.37} = 1.171$, $p = 0.34$, $\eta^2 = 0.013$, $1-\beta = 0.091$). As the main effect of the trials was significant, I conducted post hoc analysis (with Bonferroni correction), and the results revealed that the SD of the frequency up to 10 trials was significantly larger than the others, except for up to 20 trials. (*ps* < 0.0013, *ds* > 0.74). This result indicates that the SD of the frequency decreased initially and did not change thereafter.

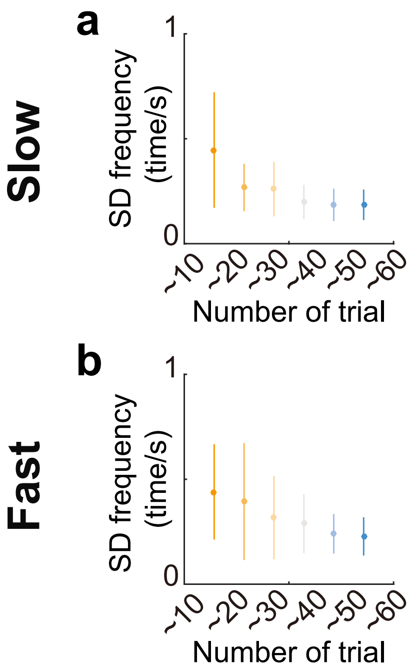

Figure 3-4 Cumulative changes of standard deviation in frequency

(a, b) Cumulative changes in the group data of the standard deviation (SD) of the frequency of direction changes in each *X* column (a) in the slow condition and (b) in the fast condition. Each color represents the accumulated data up to each trial.

Figures 3-5a and c show the mean response times of the defender to the direction changes of the attacker at each position. A two-way (condition and *X* position) repeated measures ANOVA revealed that the main effects and the interaction were not significant (Figures 3-5b and f; $F_{1, 11} = 2.37, p = 0.15, \eta^2 = 0.047, 1-\beta = 0.58$; $F_{1.52, 16.69} = 0.69, p = 0.48, \eta^2 = 0.013, 1-\beta = 0.11$; $F_{3, 33} = 1.68, p = 0.19, \eta^2 = 0.014, 1-\beta = 0.10$). Figures 3-6a and c show typical histogram examples of the response times of the defender in each of the 10 trials, which competed with the participant in Figure 3-3a and b, respectively. A two-way (condition and trials) repeated measures ANOVA revealed that the main effects and the interaction were not significant (Figures 3-6b and d; $F_{1,\,11} = 2.31$, $p = 0.16$, $\eta^2 = 0.047$, $1-\beta = 0.75$; $F_{5,\,55} = 0.641$, $p = 0.67$, $\eta^2 = 0.0094$, $1-\beta = 0.12$; $F_{5,\,55} = 1.141$, $p = 0.35$, $\eta^2 = 0.013$, $1-\beta = 0.11$).

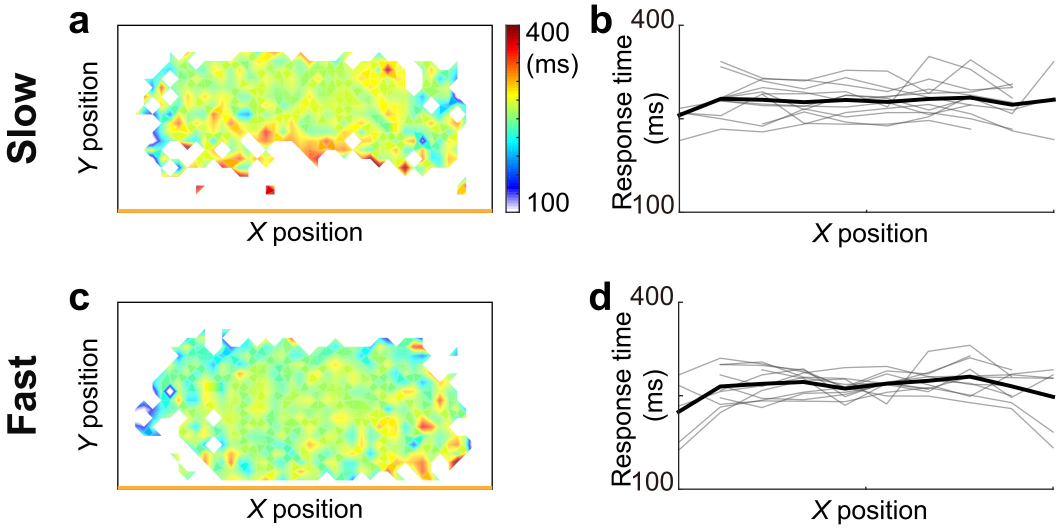

Figure 3-5 Response time to spatially characterized direction changes

(a, c) Mean response times of the defender in each position from all trials (a) in the slow condition and (c) in the fast condition. The court was divided into 968 (44 × 22) cells of 30 square pixels each. (b, d) The mean response time in *X* position of each participant. In this case, the *X* position was divided into 10 columns.

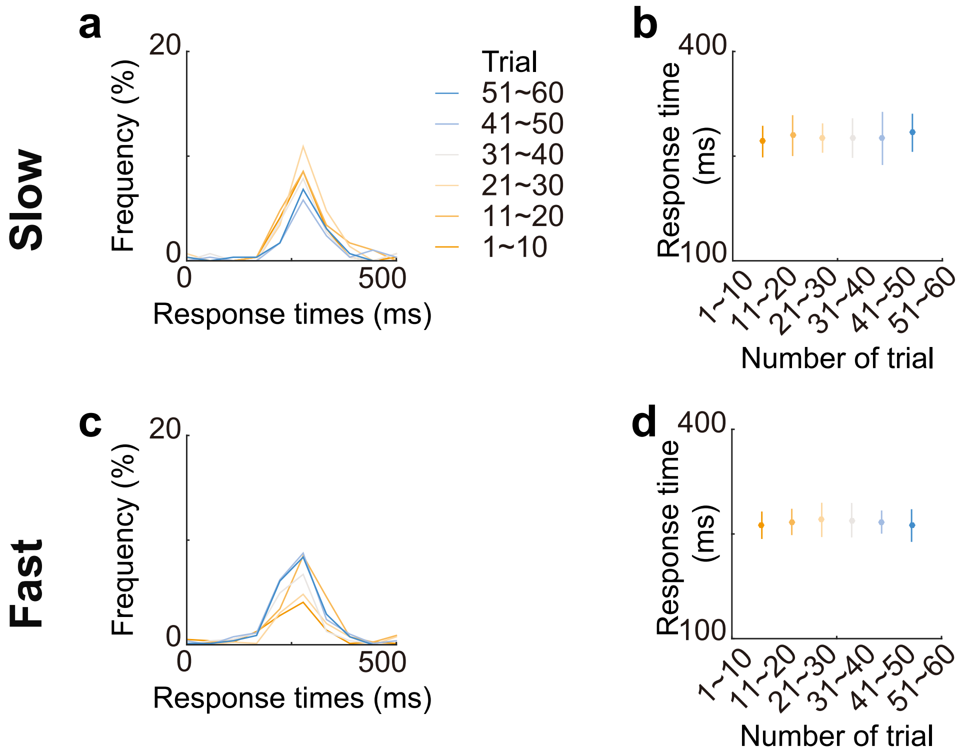

Figure 3-6 Change of response time over time

(a, c) The histogram of the response time over time in typical defender (a) in the slow condition and (c) in the fast condition. Each color represents a total of 10 trials. (b, d) The group data of the mean response time in each of the 10 trials over time (b) in the slow condition and (d) in the fast condition.

I next examined the time interval of the direction changes of the attacker. Figures 3-7a and c show the relative frequency of direction change times from the previous direction change time. The distributions were bimodal in both conditions, and thus I classified the directions changes into two types: short-interval and long-interval (red and blue parts in Figures 3-7a and c, respectively). The boundary between them was 350 ms in both conditions (see Methods).

For the response time of the defender to the direction change of the attacker, a two-way (condition and time interval) repeated measures ANOVA revealed a main effect of time interval (Figure3-8; $F_{4,\ 40}$ = 17.2, p = 2.8×10^{-8}, η^2 = 0.32, $1-\beta$ = 1.0). The condition and the interaction between these factors were not significant ($F_{1, 10} = 0.80$, $p = 0.39$, $\eta^2 = 0.0059$, $1-\beta = 0.13$; $F_{1.62, 40} = 0.31$, $p = 0.69$, $\eta^2 = 0.0053$, $1-\beta = 0.063$). As the main effect of trials was significant, I conducted post hoc analysis (with Bonferroni correction), and the results revealed that the response time of the defender to the short-interval direction changes of the attacker was significantly greater than to the others ($ps < 1.7\times10^{-6}$, $ds > 1.4$). The response times to the direction change with short-interval and with long-interval were 317 ± 45 and 270 ± 20 ms in the slow condition, and those were 304 ± 25 and 264 ± 17 ms in the fast condition, respectively. The short-interval direction change positions were distributed more in the center of the field compared with those with long intervals (Figures 3-9; $p = 2.1\times10^{-33}$).

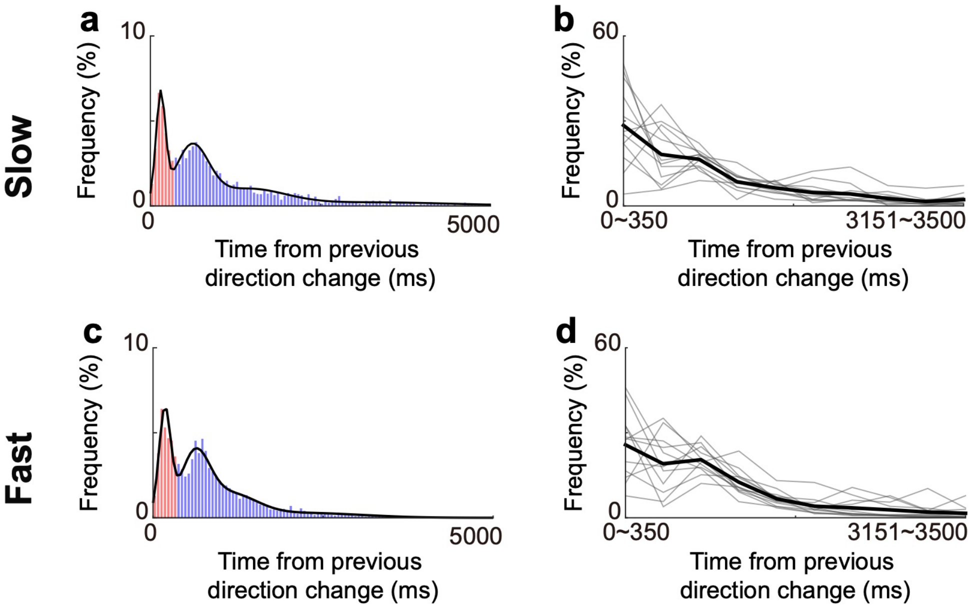

Figure 3-7 Temporal characteristics regarding direction changes

(a, c) The relative frequency (probability distribution) of time delays from the previous direction change (a) in the slow condition and (c) in the fast condition. The direction changes were classified into short-interval (red) and long-interval (blue) at 350 ms. (b, d) Histograms of the time delay from the previous direction change of each participant. The time range was set from 0 to 3500 ms, and the range was divided into 10 separate time bins.

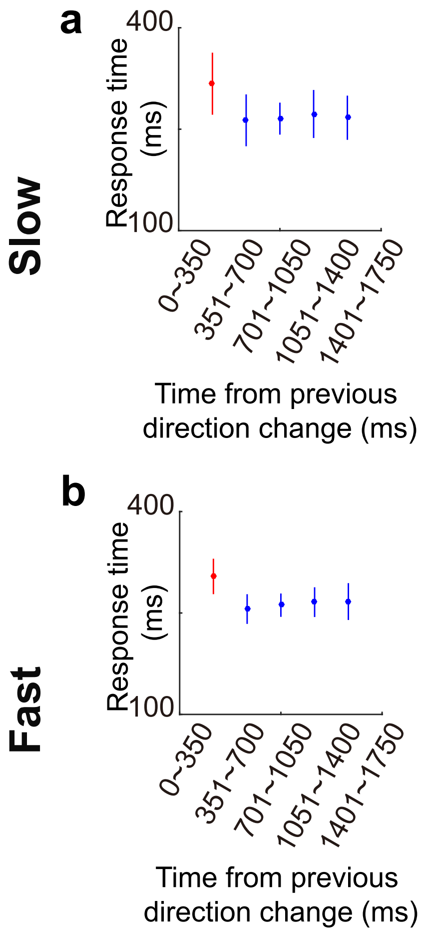

Figure 3-8. Response time to temporally characterized direction changes

(a, b) The group data of the mean response time in each time bin (a) in the slow condition and (b) in the fast condition. To exclude time bins containing a small number of data, the range of the time bins was limited from 0 to 1750 ms.

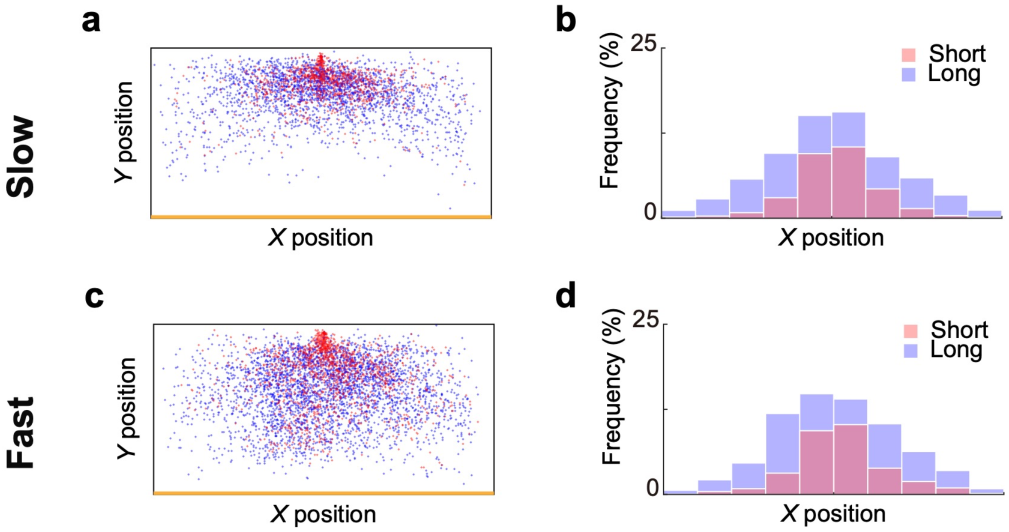

Figure 3-9 Spatial distribution of temporally characterized direction changes

(a, c) The points of short-interval direction changes (red) and long-interval direction changes (blue) from all trials (a) in the slow condition and (c) in the fast condition. (b, d) The histograms of the short-interval direction changes (red) and the long-interval direction changes (blue) at each *X* position (b) in the slow condition and (d) in the fast condition.

3.4 Discussion

Here, I explore how agents make their decisions in complex interactions such as those seen in a variety of sports situations. In this study, I focused on the probability distribution regarding direction changes in chase-and-escape interactions and elucidated the corresponding spatiotemporal characteristics. For the spatial aspect, the frequency of direction changes of the attacker (evader) was almost uniformly distributed. On the other hand, for the temporal aspect, the relative frequency of direction changes of the attacker showed a bimodal distribution.

The frequency of direction changes of the attacker at each position on the court was approximately uniform. This spatial uniformity means that the probability of the evader changing or not changing its movement direction was almost constant regardless of its position on the court. This characteristic would be useful for the attacker to maximize the uncertainty in its direction change. The bias of the frequency of attacker's direction changes rapidly approached a uniform distribution over time. This result indicates that the predictability for the defender using spatial probability information does not improve, even if information on the direction changes of the attacker had been accumulated. As a result, it would be difficult for the defender to anticipate in which direction the attacker would change its movement. Our results show that the proportion of direction change converging to a certain value is similar to matching pennies, in which players stochastically choose between two alternatives (heads or tails) with 50% in a mixed strategy Nash equilibrium in the framework of Game Theory (Abreu & Rubinstein, 1988; Nash, 1950; Rubinstein, 1991). These results suggest that the attacker randomizes its own actions so that they cannot be predicted by the defender.

The response time of the defender to the direction change of the attacker did not differ according to the position on the court and did not shorten over time. These results suggest that it would be difficult for the defender to respond predictively to the attacker's direction change using situational probability information and support the idea that action selections with equal probabilities increase unpredictability against the opponent (Abreu & Rubinstein, 1988; Nash, 1950; Rubinstein, 1991). Note that some results, such as the frequency of the direction change did not differ in X position and the response time of the defender did not differ in X position and over time, have low powers and thus further research would be necessary to ensure these findings. On the other hand, these results were approximately consistent between participants (see Figures S3-1 to 4).

The relative frequency of the time interval in direction changes of the attacker showed a bimodal distribution. The peak of the distribution of short-interval direction changes was 200 ms, which, assuming that the human visuo-motor delay is 200–300 ms, is not enough time for the attacker to gain feedback regarding the defender's response to its own action(Hoff & Arbib, 1993). Thus, this short-interval direction change (i.e., two consecutive directions) would be a feedforward control. In this case, the movement direction of the attacker in the *X* direction is the same as the original movement direction (i.e., right to left to right or vice versa), and thus, if the defender does not respond to the first direction change, the situation worsens for the attacker. Consequently, to execute two consecutive direction changes, the attacker relies on the defender responding to the first direction change. On the other hand, for long-interval direction changes, the attacker has enough time to gain feedback and can take into account the observed information regarding the defender's response. In addition, the shapes of bimodal distribution were somewhat different between individuals but were approximately consistent within individuals, namely, between conditions (see Figures S3-5 and 6). This may reflect an individual playing preferences or habits.

The defender's response to the attacker's short-interval direction change was delayed compared with the response to long-interval changes. Generally, it has been shown that humans respond quickly to frequent stimuli (Hyman, 1953). Based on this finding, the response time of the defender to short-interval direction changes should shorten, but contrarily, the response time lengthened in this study (see also Figures S3-7 and 8). One possible cause for this extra response delay is an interference of sensorimotor processing. In the double-stimulation paradigm, a phenomenon called the psychological refractory period has been demonstrated, in which the second response is delayed for two consecutive stimuli (Pashler, 1994; Smith, 1967; Telford, 1931; Welford, 1952; Zylberberg et al., 2012). It is thought that this phenomenon is caused by overlapping of the response to the first stimulus and the response to the second stimulus. Because inter-stimulus intervals were distributed around 200 milliseconds in the short-interval direction changes, a similar delay may occur to the defender's response. In addition, it should be noted that, because the long-tailed distribution of long-interval changes increases the mean direction change time interval, this bimodal distribution can enhance the psychological refractory period effect by decreasing the temporal predictability of the direction changes. Interestingly, the temporal characteristics in bimodal distribution, which is a high frequency of direction change with short-interval and a long-tail of that with long intervals were more prominent in the group with high attack success rate than that with low attack success rate (see Figure S3-9).

Our experiment was different from sport situations in several points. One was the viewpoint, that is, egocentric view in sport situations and bird's eye view in our computer-based task. For example, in sport situations, when an attacker changes movement direction, the position of image would move from left to right (or vice versa) in the defender's field of view. On the other hand, in our task, the position of the image in the field of view is little changed. That is, the body of defender acts as a reference frame in sport situations and does not act in our task. This difference in visual information could affect cognitive processing (e.g., S-R associations (Hommel, 1993, 1994; Hommel & Lippa, 1995; Lamberts, Tavernier, & D'Ydewalle, 1992; Simon, Acosta, Mewaldt, & Speidel, 1976)) and could change the response time of defender. Another was the kinematic factors, that is, whole body movement in sport situations and finger movement in our task. In general, direction changes in locomotion are mechanically constrained (Brault et al., 2010, 2012; Dickinson, 2000; Fujii, Yoshioka, Isaka, & Kouzaki, 2015), and it cannot change movement direction suddenly in sport situations, unlike our task. This difference in mechanical constraints also could affect their interaction. Thus, further considerations by integrating sensory and motor factors would be necessary for a better understanding of effective attack behaviors in sport situations.

3.5 Summary

In summary, our results showed that the evader's decisions regarding direction changes have two characteristics: spatial uniformity and temporal bimodality. The former result is consistent with the findings of non-human studies that suggested the effectiveness of a strategy that increases unpredictability (Domenici, Blagburn, & Bacon, 2011b; Humphries & Driver, 1970), indicating that an element of unpredictability is key to successful escape across species. The latter result indicated that the attacker repeated effective behaviors (i.e., two consecutive direction changes), which lengthened the defender's response time. Our results suggest that these characteristics could be useful for preventing the pursuer's predictive response and to gain the benefit of an extra response delay of tens of milliseconds.

Chapter 4 Study 3

Underlying structure in the dynamics of chase and escape interactions

This study has been published as:

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4.1 Introduction

Chase and escape behaviors are fundamental skills in many sports and are crucial for the survival of many animals in the wild making them highly important behaviors (Clark, 1958; Howland, 1974; Packard, 1969; Wei et al., 2009; Weihs & Webb, 1984b). A number of factors, such as strategy, kinematic ability, and surroundings, are involved in determining the outcome (i.e., successful escape or interception) (Domenici et al., 2011a, 2011b), which makes any explanation of these behaviors complex.

Geometrical models have provided a framework for determining the conditions for escape success (Arnott et al., 1999; Corcoran & Conner, 2016; Domenici, 2002; Howland, 1974; Weihs & Webb, 1984b). For example, a model of the initial phase of escape behavior shows what escape angle is needed to reach a safety zone, based on the kinematic parameters such as speeds of prey and predator and distance between these two agents (timing of the escape response) (Domenici, 2002). In addition, models of aerial sequential escape behavior have shown that speeds, turn rates (minimum turning radii), and distance between agents are important determinants of success for prey attempting to reach a safety zone that flanks either side of an approaching predator (Corcoran & Conner, 2016; Howland, 1974). Although these models make assumptions for simplicity, such as evader and pursuer move at constant speed, the predictions are consistent with observed escape behaviors in some cases (Corcoran & Conner, 2016; Domenici et al., 2011a, 2011b). These findings have shown the usefulness of geometric models, but the effectiveness of such models for human chase-and-escape behaviors is unknown.

In sports, chase-and-escape behaviors (i.e., one-on-one) have been studied, focusing on the positional relationship between two agents, attacker and defender (Araújo et al., 2014; Davids et al., 2015; Duarte et al., 2012; Esteves et al., 2012; Passos et al., 2006, 2009; Vilar, Araújo, Davids, & Button, 2012). In these studies, chase-and-escape behaviors have been described as the change of bearing angle, which is the angle between the range vector (defender to attacker) and the *X*-axis (mediolateral direction) in an absolute coordinate system (Figure 4-1a). In sports, chase-and-escape behaviors are often performed by agents of similar speed and maneuverability, as players are generally matched with opponents belonging to the same category (e.g., junior-junior and professional-professional). Thus, once an attacker passes a defender, the attacker is rarely overtaken by the defender. As a result, I can assume that the escape success is achieved when the bearing angle becomes less than 0 degrees, or more than 180 degrees (Passos et al., 2013). This approach can simplify complex chase-and-escape behaviors that involve multiple turns. However, although previous studies have presented certain kinematic parameters that could be important (Araújo et al., 2014; Duarte et al., 2010; Fujii, Isaka, et al., 2015; Passos, Araújo, Davids, Gouveia, et al., 2008; Vilar et al., 2014), the relationship between these parameters and the determinants of chase-and-escape outcomes remains unclear.

In this study, I examined the determinants of chase-and-escape outcomes, based on kinematic parameters. The key parameters, such as velocity (movement speed and direction), response time (visuo-motor delay), and inter-agent distance presented by the previous studies are geometrically associated with changes in the bearing angle. In the initial phase of a maneuver, the displacement of the attacker during the defender's response time is determined by the product of the velocity of the attacker and the response time of the defender (illustrated by the yellow section in Figure 4-1a). It is obvious that this displacement changes the bearing angle (Figure 4-1b). In the later phase (where the two agents move), the change in bearing angle depends on the displacement of both the attacker and the defender. The change is smaller when agents move in the same mediolateral direction, and larger when agents move in the opposite mediolateral directions (see the second and third phases in Figures 4-1a and b). An opposite movement in the mediolateral direction is caused by the defender's visuomotor delay. The visuomotor delay, which is the latency from sensory input to motor output, is inevitable in animals and is approximately constant in humans (Franklin & Wolpert, 2011). Thus, if the speeds are larger, the displacements during the response time and the changes in the bearing angle should be larger (Figure 4-1c). That is, increased speed should make the bearing angle closer to the condition of escape success in which the bearing angle is less than 0 degrees or more than 180 degrees. In other words, the increase in speed can be advantageous for the attacker. Similarly, the increase in the response time should make the bearing angle closer to the condition of escape success and can also be advantageous for the attacker. To test these possibilities, I constructed a virtual chase-and-escape task (Figure 4-2a), which allows us to manipulate the kinematic parameters of the agents. Thus, it is possible to examine the effects of certain manipulated parameters on individual behaviors and interaction outcomes. Specifically, I manipulated the speeds of agents in Experiment 1, and the response time of defenders in Experiment 2. In both experiments, the attacker was required to move past the defender and reach the end line behind the defender, and the defender was required to catch the attacker (Figure 4-2b). In the first experiment, I showed that the escape (attack) success is more frequent with increase in speed. Then, in the second experiment, I confirmed that the escape success is more frequent with increase in response time.

The contributions of this study are (i) to show the importance of the relationship between speed and visuo-motor delay in chase-and-escape interactions in sports, (ii) to obtain suggestions that these parameters may determine the outcome of situations in which evaders make sharp turns, such as terrestrial chase-and-escape interactions in animals, and (iii) to provide the insight that seemingly unconstrained individual behavior may actually be quite constrained in two-agent interactions.

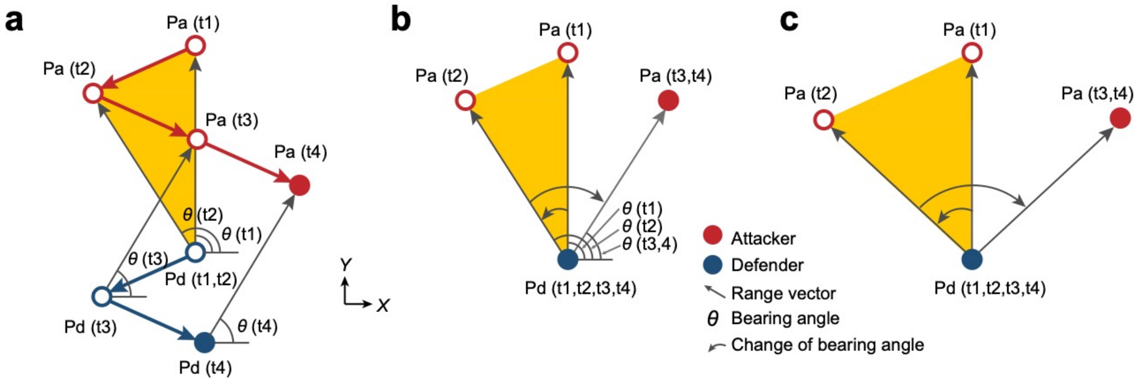

Figure 4-1 Geometrical models of attacker-defender interactions

(a) In the initial phase (t1 to t2; yellow section), the attacker moves from the starting position directly facing the defender. During this phase, the defender does not move as a result of visuo-motor delay. In the second phase (t2 to t3), the attacker changes direction, but the defender moves in the opposite direction to the attacker because they are using perceptual information from the initial phase. In the third phase (t3 to t4), the defender changes direction to move in the same direction as the attacker. (b) When the attacker and defender move as shown in (a), in the initial phase, the bearing angle increases (in this Figure, to the left). In the second phase, the change in bearing angle is twice that of the change in the initial phase, because the attacker and defender move in opposite directions in the *X*-axis during this phase. As a result, during this phase, the change in the bearing angle increases to the right. In the third phase, the bearing angle does not change because the attacker and defender are moving in parallel. (c) In a case in which the speed of the agents is increased, in the initial phase, the attacker's displacement during the visuo-motor delay is greater, and thus the change in the bearing angle is greater than in (b). As in the case of (b), the change in the bearing angle in the opposite direction is twice as great during the second phase as during the initial phase, and the bearing angle does not change during the third phase.

4.2 Methods

4.2.1 Participants

There were twelve healthy right-handed male students who exercised regularly participated in each experiment (mean age ± SD: Experiment 1, 24.9 ± 2.3; Experiment 2, 25.0 ± 2.4). The study was conducted in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the University of Tokyo of Arts and Sciences. Informed consent was received from each participant before the experiments. In both experiments, participants were recruited in pairs and each member of each pair took on the roles of both attacker and defender in turn.

4.2.2 Experimental setup

Stimuli were presented in a dimly lit room on a 15.5 in (34.3 × 19.3 cm) screen. The participants were seated at a viewing distance of 50 cm. A partition prevented direct viewing of the other player's hands. Data on the positions of the attacker and defender were recorded on a computer (Sony SVF152C16N) running Psychtoolbox 3.0 software at a frequency of 60 frames per second, and a resolution of 1366 × 768 pixels.

4.2.3 Experimental design

Participants interacted with the task using Xbox One controllers (Figures 2a and b). The dimensions of the court onscreen were 33.1 cm × 16.6 cm (width × height). Each participant controlled either a red disk representing an attacker or a blue disk representing a defender on the screen. The diameter of each disk was 1.0 cm. The objective of the attacker was to get past the defender and reach the end line (a yellow line) behind the defender, whereas the objective of the defender was to catch the attacker. I regarded a “catch” as a situation in which the outer edges of the disks were in contact. If the attacker left the bounds of the court, the trial was deemed a defensive success. The velocity of each agent was determined by the degree of inclination of the joystick on their respective controller. In preliminary experiments, I tested the agents at various speeds (e.g., attacker speed: defender speed = 1,0: 0.7, 0.8, 0.9, 1.0, 1.1, 1.2 or 1.3). If there were a speed difference between the agents, the faster one had a distinct advantage, and it was difficult for slower one to keep his or her motivation. Thus, in each experiment, I made the maximum speed of the attacker and the defender equal. The experimental task began with a start cue. No additional instruction, such as a time limit, was given to participants. To provide feedback on the result of each trial, when the attacker reached the end line (a successful attack), a high-pitched beep was played. Conversely, when the defender caught the attacker or the attacker left the bounds of the court (a successful defense), a low-pitched beep sounded. The number of successful attacks was indicated at the end of each block; blocks consisted of 30 trials. There were 40 warm-up trials and 240 experimental trials per pair of participants. For the experimental trials, each participant controlled the attacker and defender for 120 trials each. Experimental trials were presented in eight blocks. The role of each participant was randomized between blocks, and the experimental condition was randomized between pairs.

4.2.4 Experimental conditions

There were two experimental conditions in each experiment. In Experiment 3, I manipulated the maximum speed of the agents (slow: 3 cm/s, vs. fast: 4.5 cm/s). In Experiment 4, I manipulated the delay between the defender’s joystick operation and movement of the onscreen agent (no-delay vs. added-delay). The duration of the delay in the added-delay condition was 133 ms. Both agents’ maximum speeds were set at 3 cm/s in both conditions in Experiment 2.

4.2.5 Data analysis

All data analysis was performed in MATLAB (MathWorks). I analyzed only the data collected while the absolute angle between the defender and the attacker was in the range 0 to 180 degrees, to exclude situations in which the defender had given up trying to catch the attacker.

4.2.5.1 Variables

The range vector was defined as the vector from the position of defender to that of attacker (Figure 4-2c). The bearing angle was defined as the angle between the range vector and the *X*-axis in an absolute coordinate system. The chase angle was defined as the angle between the range vector and the velocity vector of the defender, and the escape angle was defined as the angle between the vector from the position of attacker to that of defender and the velocity vector of the attacker. The magnitude of the range vector corresponds to the inter-agent distance.

4.2.5.2 Mean angle

The mean escape angle and mean chase angle were calculated as an average of the direction in which the attacker and defender moved in each instance, respectively, after pooling data from all trials. Each instance was defined by a pair of integers (the bearing angle and inter-agent distance in mean escape angle; and the bearing angle and escape angle in mean chase angle), and the parameters for each experimental data point were rounded to the nearest integer to bin the response into an instance.

4.2.5.3 Response time

Response time was defined as the time between a directional change in the *X*-axis velocity of the attacker and a corresponding change in that of the defender.

4.2.5.4 Direction change

A directional change was identified by a change in the sign of the *X*-axis velocity, that is, from positive to negative, or vice versa. I limited the range of response times to 0 to 750 ms and excluded any response time exceeding 750 ms from analysis.

4.2.5.5 Phase

A turning phase was defined as the 500 ms interval following a change in direction in the X-axis velocity of the attacker. A straight phase was defined as any other time during the trial.

4.2.6 Statistical analysis

To test the relationship of the mean escape angles and mean chase angles between conditions (slow and fast), I calculated correlation coefficients. In the correlation analysis, I extracted data from all trials for situations in which the mean angle appeared in both conditions, and I used circular correlation coefficient ρ instead of Pearson's product-moment correlation coefficient *r* because both values were circular (Berens, 2009). For comparisons of the escape angle and chase angle between the conditions, I did not distinguish between the left and right in terms of the agent's direction of movement relative to their opponent, instead using the absolute value of the angle. For comparisons of histograms of the *Y*-axis velocity of the defender between conditions, I used the Kolmogorov-Smirnov test. For comparison of the variables between conditions and phases (straight and turning), I used paired *t*-test if the normality assumption was accepted by Lilliefors test. If rejected, Wilcoxon signed-rank test was used. To test the relationship between the bearing angle and the velocity of the defender in the *Y*-axis, I did not distinguish between left and right in measuring the size of the bearing angle. That is, I calculated the Pearson's product-moment correlation coefficient, *r*, between the degree of divergence from 90 degrees in the bearing angle and the displacement of the defender in the *Y*-axis. In this analysis, the possible values of the bearing angle were divided into nine bins of ten degrees each, and the average value of the defender's *Y*-axis velocity in each bin was calculated for each participant. Effect sizes were estimated using Cohen's *d* for *t*-test, and matched-pairs rank-biserial correlation *r* for Wilcoxon signed-rank test (Kerby, 2014); I report the absolute values of effect sizes. The statistical significance level was set at $p < 0.05$. Statistical analyses were performed using the MATLAB Statistical Toolbox (MathWorks).

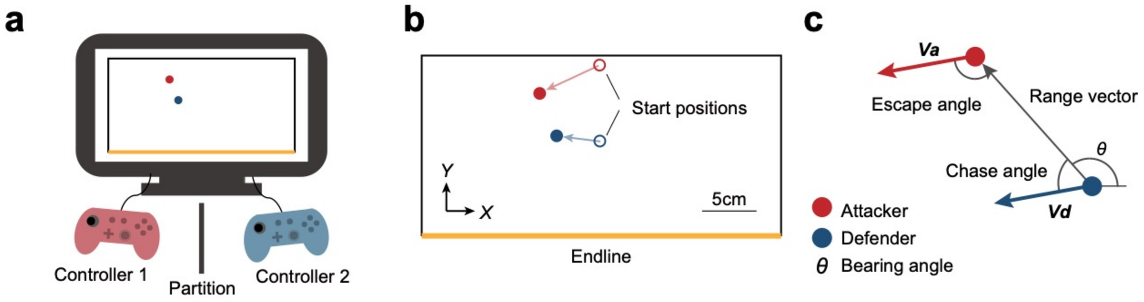

Figure 4-2 Experimental methods

(a) Participants were each seated in a chair and operated a joystick on the left side of a controller that controlled the velocity of a disk (red or blue) on a screen. A partition prevented direct viewing by each participant of the other's hands. (b) The red disk, representing the attacker, started in the upper middle of the screen. The blue disk, representing the defender, started in the center of the screen. The diameter of each disk was 1.0 cm. The attacker's goal was to reach the end line (a yellow line) located behind the defender without being caught (defined by contact between the outer edges of the disks) by the defender, whereas the defender's goal was to catch the attacker. A black rectangle surrounding the disks defined the "court" area for the task. If the attacker left the bounds of the court, the trial was deemed a defensive success. (c) I defined a range vector, pointing from the defender to the attacker. The chase angle was defined as the angle between the range vector and the velocity vector of the defender. The escape angle was defined as the angle between the inverse of the range vector (i.e., a vector pointing from the attacker to the defender) and the velocity vector of the attacker. The bearing angle (θ) was defined as the angle between the range vector and the X axis. Finally, the inter-agent distance was defined as the magnitude of the range vector.

4.3 Results

Experiment 3

In Experiment 3, I manipulated the agents' speeds of movement using two conditions. The agents' maximum speeds were set at 3 cm/s across the display in the slow condition, and 4.5 cm/s in the fast condition.

Figures 4-3a and c shows the mean escape angle in each instance (see Materials and Methods for details) in the slow and fast conditions. The distribution of the mean escape angle in each instance was similar between the slow and fast conditions, and there was statistically significant correlation ($\rho = 0.88, p < .001$; Figure 4-3e). The distribution of the mean chase angle in each instance was also similar between the conditions, and there was statistically significant correlation ($\rho = 0.60, p < .001$; Figures 4-3b, d and f). The majority of escape angles were obtuse (Figure 4-4a; slow: 66%, fast: 68%), especially if the first three seconds in each trial were excluded (slow: 85%, fast: 83%), and there was no statistically significant difference in escape angle between the conditions (t_{11}= 0.73, $p > .05$, $d = 0.30$; Figure 4-4a). This result indicated that the attacker moved away from the defender. The majority of chase angles were acute (Figures 4-4b; slow: 90%, fast: 83%), and there was no statistically significant difference in chase angle between the conditions (t_{11}= 1.95, $p > .05$, $d = 0.79$; Figure 3f). These results indicated that the attacker and the defender largely moved in parallel in both conditions.

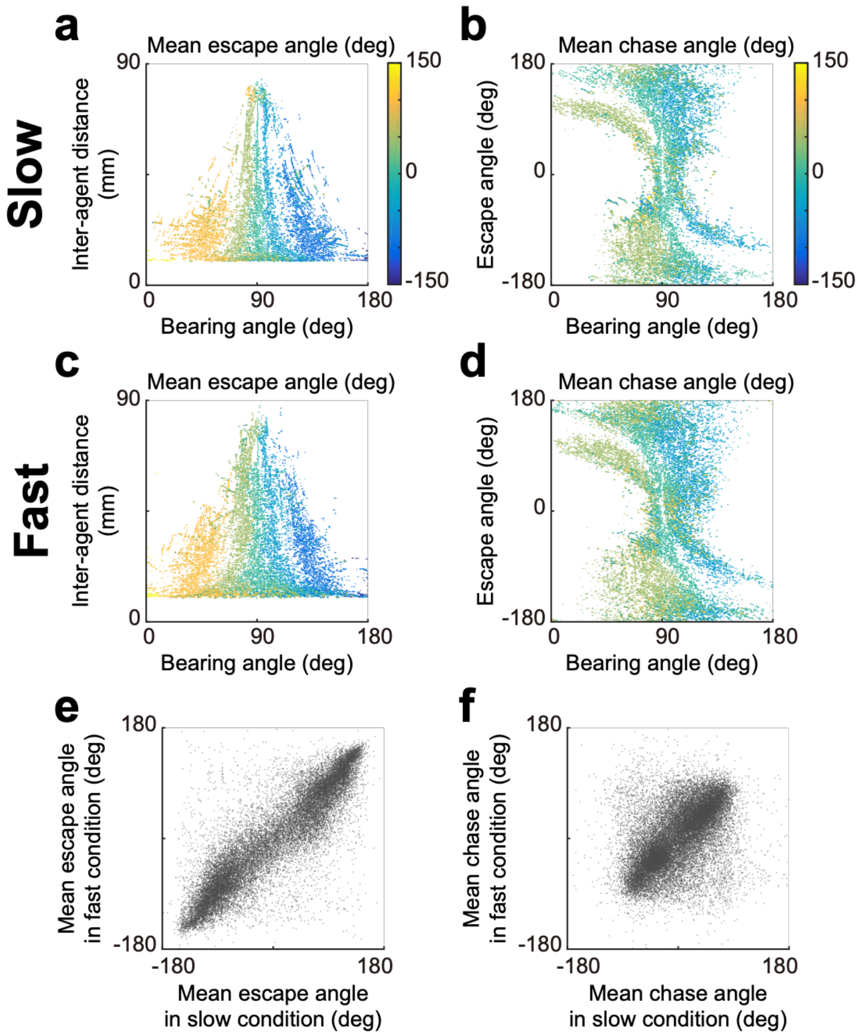

Figure 4-3 Movement direction in each instance

(a, c) Each color represents the average escape angle for a given bearing angle and inter-agent distance (a) in the slow condition and (c) in the fast condition. This is an average of the direction in which the attacker moved in each instance across all trials. (b, d) Each color represents the average chase angle for a given bearing angle and escape angle (b) in the slow condition and (d) in the fast condition. This is an average of the direction in which the defender moved in each instance across all trials. (e, f) Comparison of (e) mean escape angles and (f) mean chase angles between the slow condition and the fast condition. There were positive correlations (ρ = 0.88 in mean escape angle and ρ = 0.60 in mean chase angle).

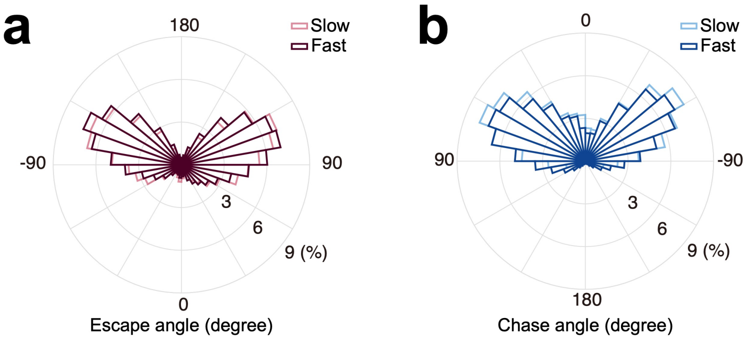

Figure 4-4 Distribution of movement direction

(a) Escape angles were mostly obtuse in both the slow condition (light red) and the fast condition (dark red). This result indicated that the attacker moved away from the defender. (b) Chase angles were mostly acute in both the slow condition (light blue) and the fast condition (dark blue). This result indicated that the defender moved toward the attacker.

Figures 4-5a and b are heat maps of the proportion of time the defender spent in each location, for each speed condition. The defender moved backward (toward the end line) to a greater extent in the fast condition than the slow condition (Figure 4-6a; $D = 0.36$, $p < .001$), and the successful interception rate was lower in the fast condition than the slow condition (Figure 4-6b; $t_{11} = 7.37$, $p < .001$, $d = 3.02$). Subsequently, I explored why these differences occurred between the conditions. I found that whether the defender advanced or retreated was associated with the bearing angle (Figures 4-7a and b; slow: $r = 0.78$, $p < .001$; fast: $r = 0.90$, $p < .001$).

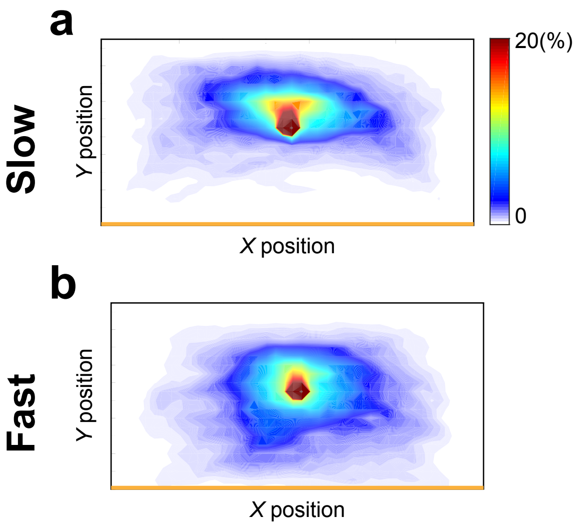

Figure 4-5 Heat map of the defender

(a, b) The heat maps show the proportion of time spent in each location of the defender (a) in the slow condition and (b) in the fast condition. The defender frequently moved forward in the slow condition, whereas frequently moved backward in the fast condition.

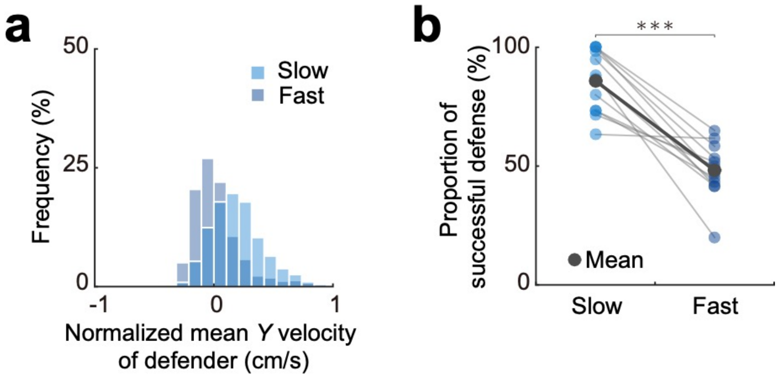

Figure 4-6 Frequency of *Y* velocity and proportion of successful defense

(a) The histogram shows the distribution of the normalized mean *Y*-axis velocity of the defender in the slow condition (light blue) and in the fast condition (dark blue). The normalized mean *Y*-axis velocity computed for each trial. The defender more frequently retreated toward the end line in the fast condition than in the slow condition. (b) The proportion of the successful defense was lower in the fast condition (dark blue) than in the slow condition (light blue).

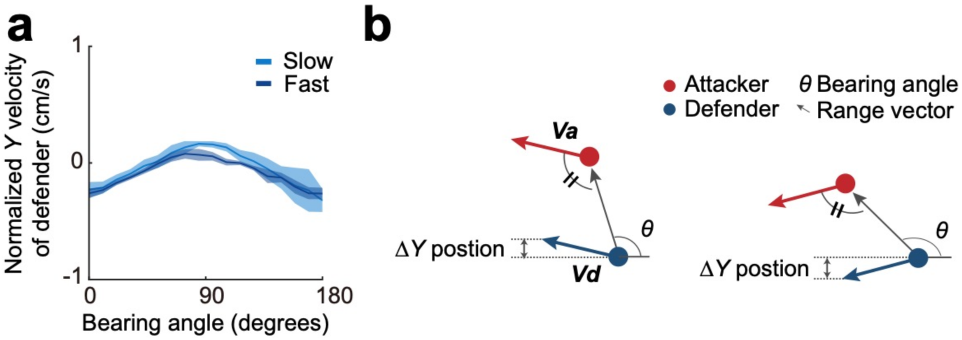

Figure 4-7 Relationship between *Y* velocity and bearing angle

(a) The relationship between the normalized *Y* velocity and the bearing angle in the slow condition (light blue) and in the fast condition (dark blue). Whether the defender advanced or retreated was associated with the bearing angle. (b) Illustrations of the advance of the defender (left side) and the retreat of the defender (right side).

The phase portraits of the bearing angle and its derivative in a representative example are presented in Figures 4-8a and b, and indicate less attraction to the center of the plot in the fast condition than in the slow condition. The rate of change in the bearing angle was greater during turning phases (i.e., when the agent was changing direction) than during straight movement phases (Figures 4-9a and b; $W = 78$, $p < .001$, $r = 1.0$). There was no statistically significant difference between conditions in the response time of the defender (Figure 4-10a; $t_{11} = 1.43$, $p > .05$, $d = 0.59$) or the inter-agent distance (Figure 4-10b; $t_{11} = 0.87$, $p > .05$, $d = 0.16$). Consequently, the variance in time in the bearing angle was greater in the fast condition than the slow condition (Figure 4-10c; $t_{11} = 8.17$, $p < .001$, $d = 2.41$).

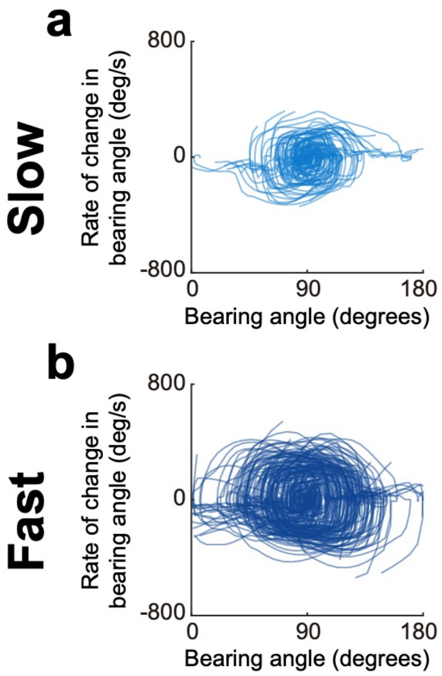

Figure 4-8 Phase portraits in typical dyad

The phase portraits of the bearing angle and its derivative in typical pair (a) in the slow condition and (b) in the fast condition. The bearing angle less attracted to the center of the plot in the fast condition than in the slow condition. Each figure consists of overlaid trajectories from a single experimental block (30 trials).

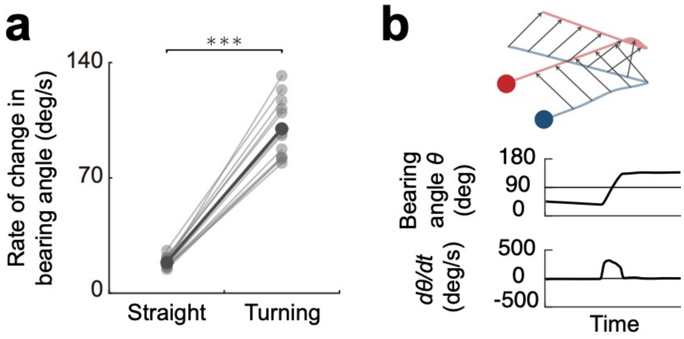

Figure 4-9 Change rate in the bearing angle in each phase

(a) The change rate in the bearing angle was greater during turning phases than during straight movement phases. (b) Illustration of part of the trajectories in an example trial, accompanied by time-series data on the bearing angle and its derivative in the trial. The change rate increased during the turn.

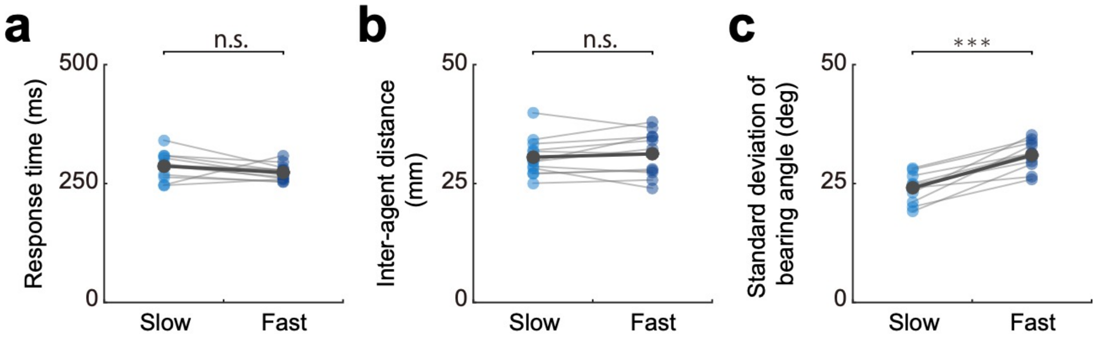

Figure 4-10 Comparison of each variable

(a) The response time of the defender to the attacker did not differ significantly between conditions. (b) The inter-agent distance also did not differ significantly. (c) The standard deviation of the bearing angle was greater in the fast condition than the slow condition.

Experiment 4

I conducted a second experiment consisting of a normal-delay condition and an added-delay condition. In both conditions, the maximum speed of both agents was set at 3 cm/s. In the added-delay condition, I artificially added a 133 ms delay to the defender's response. Specifically, the delay occurred between the participant's operation of the joystick and the movement of the defender on the screen (Figure 4-11).

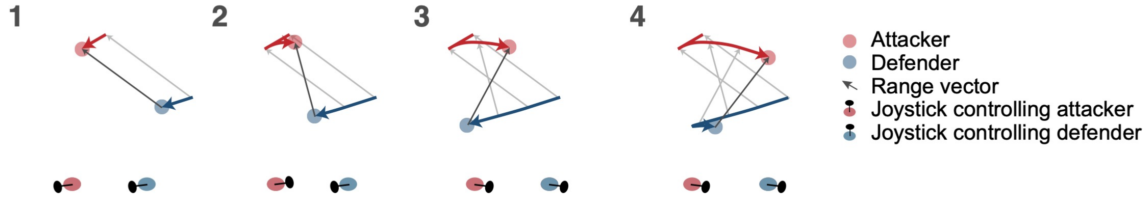

Figure 4-11 Illustration of the added-delay manipulation

(1) The attacker and the defender each move toward the left side. (2) The attacker changes direction from left to right in conjunction with the participant's operation of the joystick. (3) The participant controlling the defender responds (by operating the joystick) to the attacker’s change in direction following the visuo-motor delay. However, their operation of the joystick is not reflected immediately in the defender’s movement. (4) The defender now changes direction from left to right. The elapsed time between the attacker’s change in direction and the defender’s change in direction is the sum of the visuo-motor delay and the additional, artificially-added delay.

Figures 4-12a and b show heat maps of the defender’s position. The defender moved backward to a greater extent in the added-delay condition than the normal-delay condition (Figure 4-13a; $D = 0.59$, $p < .001$), and the successful interception rate was also lower in the added-delay condition (Figure 4-13b; $W = 78$, $p < .001$, $r = 1.0$). The Y-axis displacement of the defender was associated with the bearing angle for both conditions (Figure 4-14; normal-delay: $r = 0.66$, $p < .001$; added-delay: $r = 0.89$, $p < .001$).

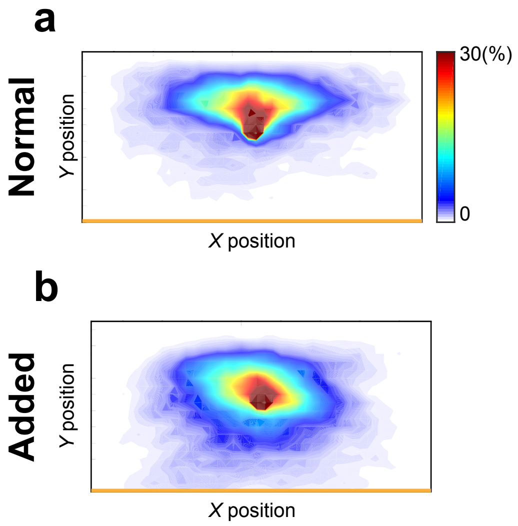

Figure 4-12 Heat map of defender

(a, b) The heat maps show the proportion of time spent in each location of the defender (a) in the normal-delay condition and (b) in the added-delay condition. The defender frequently moved forward in the normal-delay condition, whereas frequently moved backward in the added-delay condition.

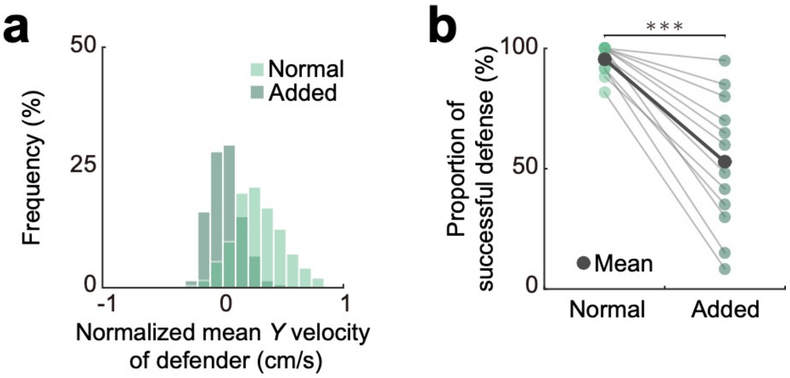

Figure 4-13 Frequency of *Y* velocity and proportion of successful defense

(a) The histogram shows the distribution of the normalized mean *Y*-axis velocity of the defender in the normal-delay condition (light green) and in the added-delay condition (dark green). The normalized mean *Y*-axis velocity computed for each trial. The defender more frequently retreated toward the end line in the fast condition than in the slow condition. (b) The proportion of the successful defense was lower in the added-delay condition (dark green) than in the added-delay condition (light green).

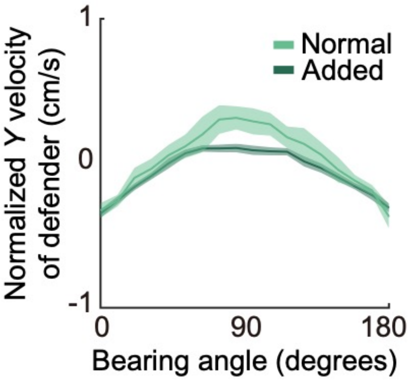

Figure 4-14 Relationship between *Y* velocity and bearing angle

The relationship between the *Y* velocity and the bearing angle in the normal-delay condition (light green) and in the added-delay condition (dark green).

The rate of change in the bearing angle was greater during turning phases than during straight movement phases (Figure 4-15; $W = 78$, $p < .001$, $r = 1.0$). Although the defender's response time was increased in the added-delay condition (Figure 4-16a; t_{11}= 34.40, $p < .001$, $d = 4.79$), there was no statistically significant difference between the conditions once this artificial addition was subtracted (Figure 4-16a; t_{11}= 1.30, $p > .05$, $d = 0.18$). The inter-agent distance was significantly smaller in the added-delay condition than in the normal-delay condition (Figure 4-16b; t_{11}= 2.78, $p < .05$, $d = 0.64$), and the variance in time in the bearing angle was greater in the added-delay condition than in the normal-delay condition (Figure 4-16c; t_{11}= 13.14, $p < .001$, $d = 2.90$).

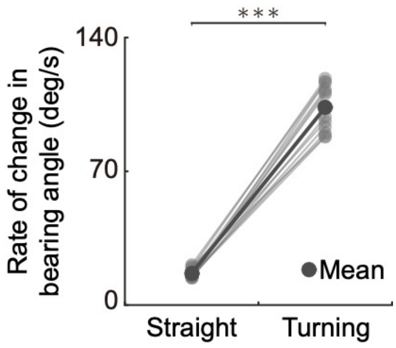

Figure 4-15 Change rate in bearing angle in each phase

The change rate in the bearing angle was greater during turning phases than during straight movement phases.

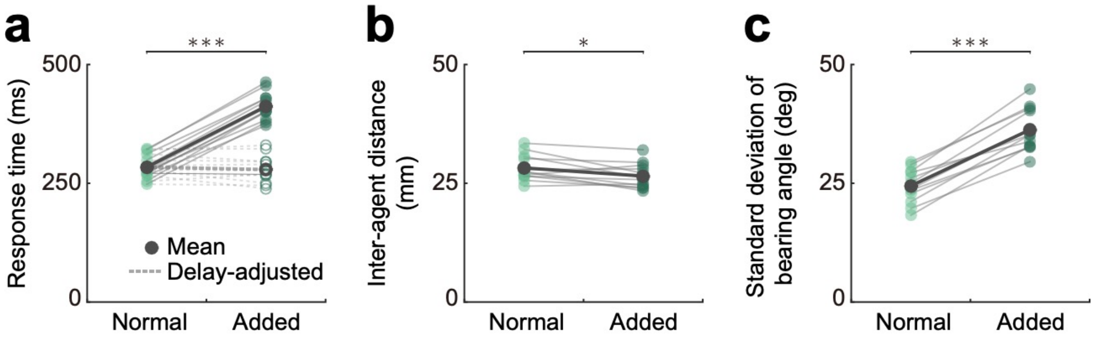

Figure 4-16 Comparison of each variable

(a) Response time was increased when an artificial delay was added (see Methods). However, there was no significant difference between the conditions when the duration of the artificially-added delay was subtracted. (b) The inter-agent distance did not differ significantly between conditions. (c) The standard deviation in of the bearing angle was greater in the added-delay condition than the normal-delay condition.

4.4 Discussion

I investigated how escaper (attacker) and chaser (defender) move and what determines the outcome of a human chase-and-escape behavior. I found that the attacker and defender moved in parallel during straight phases of movement (Figure 4-4), whereas their positional relationship (the bearing angle) changed during turning phases (Figures 4-9 and 15). This change in the bearing angle was crucial for each agent's success, and an increase in each of the two parameters manipulated here, namely the speed of movement of the agents (Experiment 3) and the defender's response time (Experiment 4), induced a larger change in the bearing angle (Figures 4-8, 10c, and 16c).

In this study, the attacker's goals were (i) to avoid being caught by the defender and (ii) to reach the end line behind the defender. The attackers largely moved at an obtuse angle with respect to the position of the defender. This strategy was in line with the first goal, but seems to work against the second goal. It should be noted that the attacker was able to simultaneously satisfy both the objectives by tilting the bearing angle on trials in which interception was successfully evaded (see right panel of Figure 4-7b).

Conversely, the defender's goals were (i) to prevent the attacker from breaking past them to reach the end line and (ii) to catch the attacker. One way to achieve these two objectives was to adopt the strategy of maintaining a constant bearing angle. In this strategy, the defender takes a trajectory such that the bearing angle remains constant, while their distance from the attacker is reduced (Fajen & Warren, 2007; Nahin, 2012). This strategy should theoretically be impossible to beat if the defender can move at a speed equal to or faster than the attacker, without a visuo-motor delay. Indeed, many animal species actually use this strategy in hunting prey (Ghose et al., 2006; Kane et al., 2015; Mischiati et al., 2014; Olberg et al., 2000). Our finding that the defender tended to move in parallel with the attacker suggests that our human defenders also used this strategy, but they could not reduce the inter-agent distance because the maximum speeds of the agents were equal in this task.

The individual behaviors adopted by the agents were independent of the agents' speeds and the defender's response time. Previous research has shown that the relative velocity and inter-agent distance affect the outcome of chase-and-escape interactions in sports (Araújo et al., 2014; Duarte et al., 2010; Fujii, Isaka, et al., 2015; Passos, Araújo, Davids, Gouveia, et al., 2008). In Experiment 1, we manipulated the maximum speeds of the agents, and observed that an increase in speed increased the relative velocity during turning phases. In these cases, there are two geometrically possible ways for the defender to reduce (or prevent) this change in the bearing angle. One is to increase the inter-agent distance, and the other is to reduce their response time (e.g., by predicting the attacker's changes of direction and responding accordingly). However, our results showed that changes in the inter-agent distance and response time were inadequate to offset the effect of a change in the agents' speeds. These results suggest that, in this type of interaction, agents' behaviors are constrained by agent-environment interactions (Davids, Button, Araújo, Renshaw, & Hristovski, 2006; Travassos, Davids, Araújo, & Esteves, 2013; Warren, 2006), and few possible strategies may be available. Despite this, in competitive situations, humans seem to decide on their strategy for themselves from numerous choices that they could make.

Our manipulation of agents' speeds directly affected the outcome of chase-and-escape interactions, even though the changes of individual agents' behaviors were small. Relative velocity, a key parameter, is the difference between the velocities of the agents. It is obvious that the faster agent is at an advantage when there is a difference in speed, but even when both speeds were the same, larger absolute speed values gave a greater advantage to the attacker. This advantage arises from the relationship between speed of movement and visuo-motor delay. During turning phases, the defender responds to the attacker's change in direction, and there is a delay between perception of the attacker's change in direction and initiation of a movement in response (Brault et al., 2010, 2012; Fujii, Yamashita, Kimura, Isaka, & Kouzaki, 2015; Fujii, Yamashita, et al., 2014; Fujii, Yoshioka, et al., 2015). This delay between a sensory input and a motor output arises as a result of neural conduction and transmission in the sensorimotor system, and a latency of 200 to 300 ms is inevitable in humans (Franklin & Wolpert, 2011). During the period of the visuo-motor delay, the defender moves in the opposite direction from the attacker, and as agents' maximum absolute speed is increased, they can move further in the opposite direction over this period. Consequently, when the inter-agent distance is held constant, the change in the bearing angle during turning phases increases with the absolute speed of movement of the agents. As a result, attackers could be more likely to escape at higher speeds.

A similar change in the chase-and-escape interaction was observed with the manipulation of the defender's visuo-motor delay. As mentioned above, during turning phases the agents moved in opposite directions. Here, the displacement between the agents is equal to their velocities multiplied by the defender's response time. In other words, both an increase in the agents' speeds of movement and an increase in the defender's response time cause an increase in the displacement. An increase in the defender's response time is geometrically comparable to an increase in the agents' speeds of movement during this phase of displacement, and could cause a similar change to chase-and-escape outcomes. In Experiment 4, I manipulated the defender's response time. As expected, the outcomes of their behaviors were affected in a similar way to Experiment 3 (compare Figure 4-5 with 12). These results suggest that agents' speeds of movement and defenders' visuo-motor delay (response time) are comparable in a chase-and-escape interaction. However, it is necessary to further examine the cause that the variation between participants in the defense success rate under the added-delay condition was great compared with that under the fast condition.

Our approach makes it possible to observe chase-and-escape behaviors in controlled situations of kinematic parameters, while these situations differ in some respects from the more complex chase-and-escape behaviors, such as those performed in a real environment. Firstly, in this study, an attacker and a defender were represented as disks onscreen. As many studies on sports have revealed, kinematic information relating to body parts is important, particularly in turning phases. For example, attackers try to deceive defenders with yawing upper body movements (Brault et al., 2010), whereas defenders try to predict the directional change of the attacker using the attacker's center of mass (Brault et al., 2012; Jackson et al., 2006). These differences may affect the variation in the response time including prediction. Secondly, in our approach, agents can always move at the same speed in any direction. As many researchers have shown, real chase-and-escape behaviors may be influenced by mechanical constraints such as morphological characteristics (Oliva, Medan, & Tomsic, 2007; Takeuchi, Tobo, & Hori, 2008), the preparatory state of the body (Fujii, Isaka, et al., 2015; Fujii, Yoshioka, et al., 2015), and the relationship between mass and speed (Wilson et al., 2015). Finally, energy consumption for the attacker and defender in our virtual task is small, which are unlike real chase-and-escape behaviors (Hubel et al., 2016; Shepard et al., 2013; Williams & Yeates, 2004; Wilson et al., 2013). For more detailed understanding, incorporating these factors would be necessary.

4.5 Summary

In conclusion, I found a simple structure in the dynamics of a chase-and-escape interaction, even though such dynamics appear to be complex. This simplicity arises from the consistency of individual behaviors when constrained by multiple requirements. As a result, the outcome of agents' behaviors is substantially dependent on their parameters of maneuverability. These findings may provide a comprehensive link between individual behaviors and the outcome of their interactions.

Chapter 5 Study 4

Superior effects of the environmental constraints to flexibility of agent on the behavioral outcome in chase and escape interactions

5.1 Introduction

Chase and escape behaviors are highly important for many human in sports and for the survival of many animals in nature (Clark, 1958; Howland, 1974; Packard, 1969; Wei et al., 2009; Weihs & Webb, 1984b). A number of factors are involved in the choice of behaviors and its outcome (i.e., successful escape or interception) (Domenici et al., 2011a, 2011b).

Previous studies on chase and escape behaviors in non-human have mainly investigated their chase or escape strategy. Specifically, these studies have examined which direction the agents (pursuer and/or evader) moves using the positional coordinates of them, and have revealed the behavioral rules of agents regarding the movement direction in each situation during chase-and-escape interactions. Most of these studies focus on the relationship between the two agents, but environments surrounding agents can also have an important effect on their behaviors and the outcome (Eilam, 2005; Gibson, 1950, 1979). In fact, it has been shown that, at least for some species, the presence of a shelter is important factor affecting the escape behaviors (Clark, 1993; Martín & López, 2011; Woodbury, 1986; Zani, Jones, Neuhaus, & Milgrom, 2009). However, the number of these studies is limited, and it is still largely unclear the effect of environments on the behavioral rules of the agents.

Human and non-human behaviors exhibit two complementary attributes, namely stability and flexibility, to achieve a specific goal, in interactions between agents and environments (Warren, 2006). The stability is characterized by that behaviors are consistent over time and reproducible on separate occasions. On the other hand, the flexibility is characterized by that behaviors are not locked into a rigid solution but tailored to current environmental conditions. These attributes in non-human chase-and-escape interactions have been observed and discussed (Evans et al., 2019; Olberg et al., 2000), but it is a lack of behavioral evidences perhaps because it is difficult to compare the behaviors under controlled experimental conditions in non-human studies.

Thus, in this study, I examined whether and how the environmental constraints affect on the behaviors and the outcomes, for human chase-and-escape interactions, based on the findings in Studies 1 to 3. Specifically, I gave the spatial and temporal constraints, which is dominant environmental constraints in human chase-and-escape behaviors (i.e., one-on-one behaviors in sports such as football, rugby, and basketball) to the agents. That is, the attacker and the defender play in different court size among these sports events, and, once either team scores and leads, the opposite team is required to comeback in the remaining time.

These spatiotemporal constraints would change their strategies such as movement directions, direction change, and response time. For example, in Study 1 and 3, I showed that the defender approximately moves along the time-optimal path, but it may move toward the attacker more straightly (like classical pursuit) or may wait for the attackers to come (like side-step) when the court width is narrow. To comprehensively test these possibilities, I conducted the chase-and-escape task under spatially constrained conditions in which the court widths are manipulated (Experiment 5) and that under temporally constrained conditions in which the time-limit was given to the defender until capture (Experiment 6) and to the attacker until reach the end line (Experiment 7).

5.2 Methods

5.2.1 Participants

Twelve healthy right-handed male students who exercised regularly participated in the experiment (mean age ± SD: 25.9 ± 3.0 in Experiment 5 (spatial constraints), 25.8 ± 3.1 in Experiment 6 (temporal constraints on the defender), and 26.3 ± 3.0 in Experiment 7 (temporal constraints on the attacker). The study was approved by the Ethics Committee of the University of Tokyo of Arts and Sciences. Informed consent was received from each participant before the experiments. In these experiments, participants were recruited in pairs and each member of each pair took on the roles of both attacker and defender in turn.

5.2.2 Experimental setup

The stimuli were presented on a 27-inch monitor (ASUS SWIFT PG278Q) at 120 Hz. The central position of each disk onscreen during the trials was recorded at 120 Hz on a computer (MacBook Pro) running Psychtoolbox 3.0 software. The participants were seated at a viewing distance of 50 cm. A partition prevented direct viewing of the other player's hands.

5.2.3 Experimental design

Participants interacted with the task using Xbox One controllers (Figure 5-1). Each participant controlled either a red disk representing an attacker or a blue disk representing a defender on the screen. The diameter of each disk was 1.0 cm. The objective of the attacker was to get past the defender and reach the end line (a yellow line) behind the defender, whereas the objective of the defender was to catch the attacker. I regarded a “catch” as a situation in which the outer edges of the disks were in contact. If the attacker left the bounds of the court, the trial was deemed a defensive success. The velocity of each agent was determined by the degree of inclination of the joystick on their respective controller. In each Experiment, I made the maximum speed of the attacker and the defender equal, and the maximum speed was set to 7.0 cm per seconds onscreen. The experimental task began with a start cue. To provide feedback on the result of each trial, when the attacker reached the end line (a successful attack), a high-pitched beep was played. Conversely, when the defender caught the attacker or the attacker left the bounds of the court (a successful defense), a low-pitched beep sounded. The number of successful attacks was indicated at the end of each block; blocks consisted of 50 trials. There were 60 warm-up trials and 300 experimental trials per pair of participants. For the experimental trials, each participant controlled the attacker and defender for 150 trials each. Experimental trials were presented in six blocks. The experimental condition was randomized between pairs.

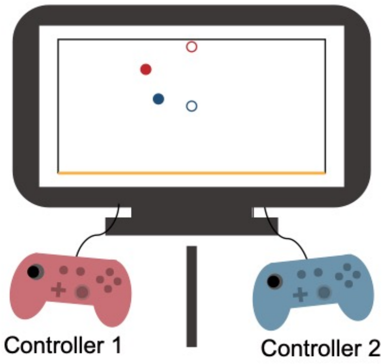

Figure 5-1 Experimental setup

Participants were each seated in a chair and operated a joystick on the left side of a controller that controlled the velocity of a disk (red or blue) on a screen. The red disk, representing the attacker, started in the upper middle of the screen (red circle). The blue disk, representing the defender, started in the center of the screen (blue circle). The diameter of each disk was 1.0 cm. The attacker's goal was to reach the end line (a yellow line) located behind the defender without being caught by the defender, whereas the defender's goal was to catch the attacker. A black rectangle surrounding the disks defined the "court" (i.e., play area) for the task. If the attacker left the bounds of the court, the trial was deemed a defensive success. A partition prevented direct viewing by each participant of the other's hands.

5.2.4 Experimental conditions

There were three experimental conditions in each Experiment. In Experiment 5, I manipulated widths of the court. The width of the court onscreen was 7.5, 15.0, 30.0 cm in narrow, square, and wide condition, respectively. The height of the court was 15.0 cm in all conditions. In Experiment 6 and 7, I gave time-limits of trials to participants controlling the defender and the attacker, respectively. In both Experiment 6 and 7, the time-limit of the trial was 10 seconds in short condition, 20 seconds in long condition, and nothing in no-limit condition. In these experiments, when the defender (attacker) could not catch the attacker (reach the end line) within the time-limit, it was regarded as the success of the opponent.

5.2.5 Data analysis

All data analysis was performed in MATLAB (MathWorks). I analyzed only the data collected while the absolute angle between the defender and the attacker was in the range 0 to 180 degrees, to exclude situations in which the defender had given up trying to catch the attacker.

5.2.5.1 Variables

The range vector was defined as the vector from the position of defender to that of attacker (Figure 2c). The bearing angle was defined as the angle between the range vector and the X-axis in an absolute coordinate system. The chase angle was defined as the angle between the range vector and the velocity vector of the defender, and the escape angle was defined as the angle between the inverse of the range vector and the velocity vector of the attacker. Response time was defined as the time between a directional change in the X-axis velocity of the attacker and a corresponding change in that of the defender. A directional change was identified by a change in the sign of the *X*-axis velocity, that is, from positive to negative, or vice versa. I limited the range of response times to 0 to 500 ms and excluded any response time exceeding 500 ms from analyses. A turning phase was defined as the 500 ms interval following a change in direction in the X-axis velocity of the attacker. A straight phase was defined as any other time during the trial.

5.2.5.2 Phase division

Initial phase was defined from the beginning of trial to 1s. In the analyses of circular histogram, I used the absolute value of chase and escape angles because these angles approximately symmetrically distributed.

5.2.5.3 Theoretically penetrable opportunity

In this analysis, I computed whether there was a theoretically penetrable opportunity in each trial. In this case, I calculated the distances from each side end of the end line (lower left and lower right corner of the court) to the attacker and defender, respectively, and calculated the difference of each distance. If the distance from one of the corners to the defender is greater than the distance from the corner to the attacker, the attacker can theoretically reach the end line without being caught by the defender. In other words, if the defender is in the overlapping part (purple part in the Figure 5-20) of the circle formed by the distance from the lower left corner to the attacker (cyan part) and the circle formed by the distance from the lower right corner to the attacker (magenta part), the defender is unbeatable. In the actual analysis, I calculated the circle radius (i.e., the distance from the corner) taking the radius of the disks into account. Specifically, the circle radius was calculated as the distance from the corner to attacker plus disk radius of the attacker plus disk radius of the defender.

5.2.6 Statistical analysis

To compare variables, one-way repeated measures ANOVA was used. In ANOVA, I tested sphericities using Mauchly's test, and, if the sphericity assumption was violated, I adjusted the degree of freedom using Greenhouse-Geisser correction ε. A paired t-test or Wilcoxon signed-rank test with Bonferroni correction was used to compare the variables within the factor where a significant effect in ANOVA. To compare the mean response time in each position, I divided the court to the two, four, and eight columns in the narrow condition, the square condition, and the wide condition, respectively. In this analysis, I compared the center two columns with no missing values between the conditions. For comparisons of the mean escape angle between the conditions, I did not distinguish between the left and right in terms of the attacker's direction of movement relative to their opponent, that is, I used the absolute value of the angle. To test the relationship between the proportion of the correct decision and the attack success rate, I calculated Pearson's product-moment correlation coefficient r. The effect size was estimated using Cohen's d for t-test, eta-squared value (η^2) for ANOVA. The statistical significance level was set at $p < 0.05$ and was adjusted using Holm–Bonferroni method in the post hoc multiple comparison. Statistical analyses were performed using the MATLAB Statistical Toolbox (MathWorks), the R version 3.5.1 (The R Foundation).

5.3 Results

Experiment 5

In Experiment 5, I gave spatial constraints to the agents. The proportion of successful attack was 0.03 ± 0.03 in the narrow condition, 0.09 ± 0.09 in the square condition, and 0.41 ± 0.22 in the wide condition, and there were statistically significant differences among conditions (Figure 5-1; $F_{1.17,\ 12.87} = 39.0$, $\eta^2 = 0.62$, $ps < 0.03$, $ds > 0.93$).

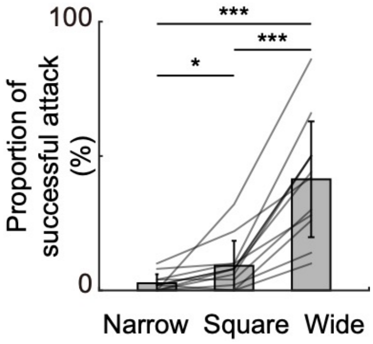

Figure 5-2 Proportion of successful attack

The proportions of successful attack were 0.03 ± 0.03 in the narrow condition, 0.09 ± 0.09 in the square condition, and 0.41 ± 0.22 in the wide condition. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Figure 5-3 shows the heat map of the position of the attacker, that of the direction change, and that of the relative frequency, in each condition. The smaller the spatial constraints, the higher the frequency of reaching close to the end line. In addition, the spatial uniformity for the relative frequency of direction change of the attacker was observed (Figures 5-3c, f, and i). This result indicates that the spatial characteristics regarding direction changes of the attacker was small among conditions.

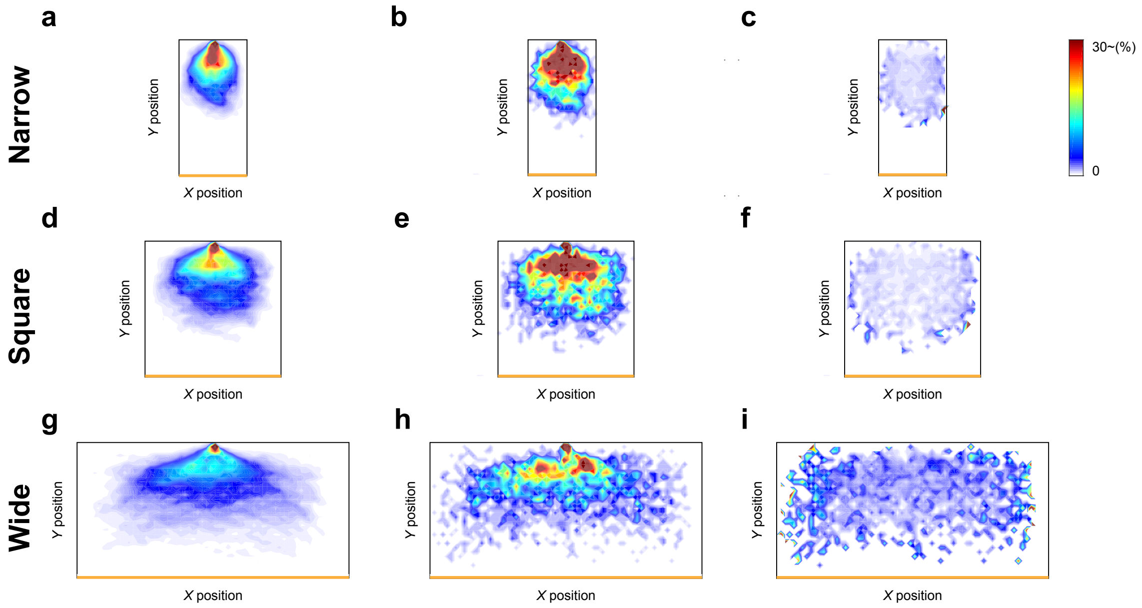

Figure 5-3 Heat maps regarding attacker

(a, d, g) The 2D-histograms of time spent of the attacker in each position (a) in the narrow condition, (d) in the square condition, and (g) in the wide condition. (b, e, h) The 2D-histograms of direction change of the attacker in each position (b) in the narrow condition, (e) in the square condition, and (h) in the wide condition. (c, f, i) The relative frequency of direction changes per time in each position (c) in the narrow condition, (f) in the square condition, and (i) in the wide condition. The court was divided into the cells of 20 square pixels each.

Figure 5-4 shows the heat map of the position of the defender and that of the response time, in each condition. The result showed that the high frequencies were distributed from the start position of the defender toward the start position of the attacker, particular in the narrow conditions (Figure 5-4a), and it indicates that the defender did not move along the time optimal path.

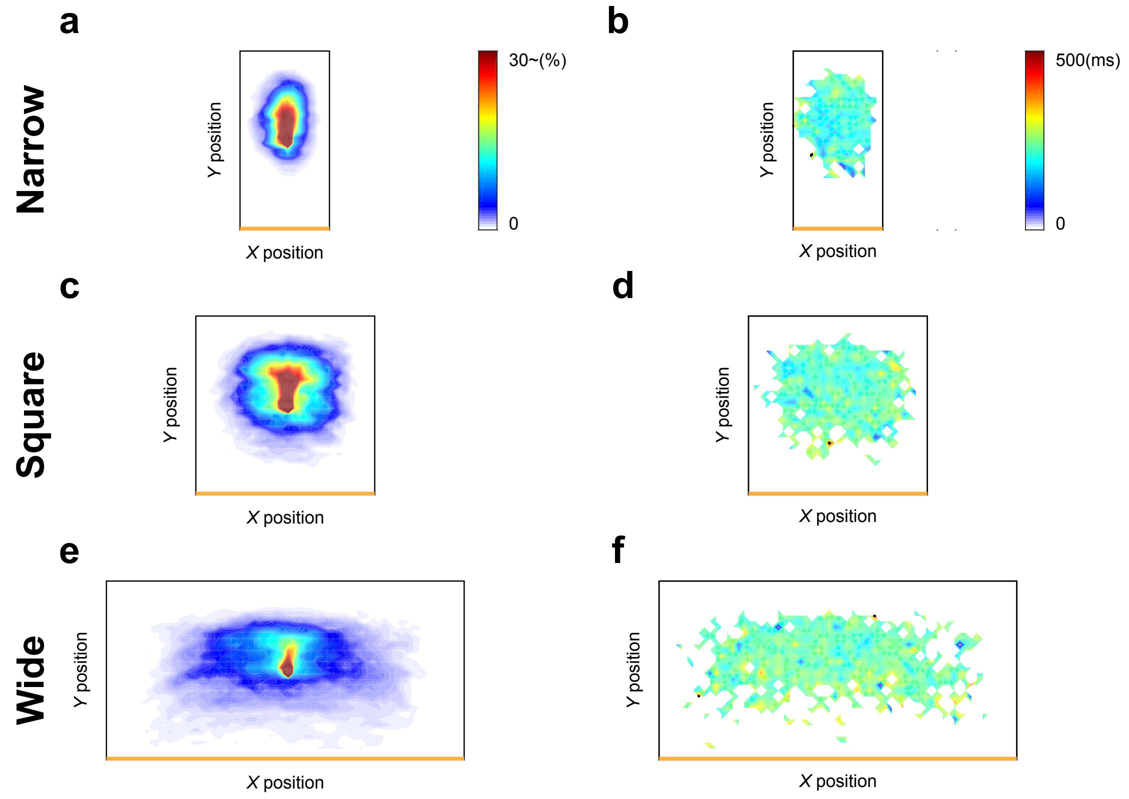

Figure 5-4 Heat maps regarding defender

(a, c, e) The 2D-histograms of time spent of the defender in each position (a) in the narrow condition, (c) in the square condition, and (e) in the wide condition. (b, d, f) The mean response times of the defender in each position (b) in the narrow condition, (d) in the square condition, and (f) in the wide condition. The court was divided into the cells of 20 square pixels each.

Thus, to quantify and visualize the fit between the observation and the prediction by the time-optical model, I computed the residuals in each tau and in each condition (Figure 5-5) and showed the heat map between the chase angles (Figure 5-6). The residuals in the bottom of residual curve were 48.0 ± 7.5 in the narrow condition, 38.3 ± 2.5 in the square condition, and 27.5 ± 3.6 in the wide condition, respectively, and a one-way repeated measured ANOVA revealed the main effect of the condition ($F_{1.16, 12.81} = 43.0$, $\eta^2 = 0.75$, $p < 0.001$). Post hoc analysis revealed that the narrower the width of court, the greater the residual ($ps < 0.05$, $ds > 1.738$). The estimated visuo-motor delays, which is the delay in the bottom of residual curve, were 246 ± 24 in the narrow condition, 253 ± 78 in the square condition, and 267 ± 36 in the wide condition, respectively, there were statistically significant differences in the estimated visuo-motor delay ($F_{2, 22} = 15.9$, $\eta^2 = 0.16$, $ps < 0.05$, $ds > 0.30$). The correlation coefficients ρ were 0.43 ± 0.16 in the narrow condition, 0.59 ± 0.09 in the square condition, and 0.74 ± 0.07 in the wide condition, respectively. These results indicate that the residuals increase and the visuo-motor delay (response time) shortened as the spatial constraints become more severe.

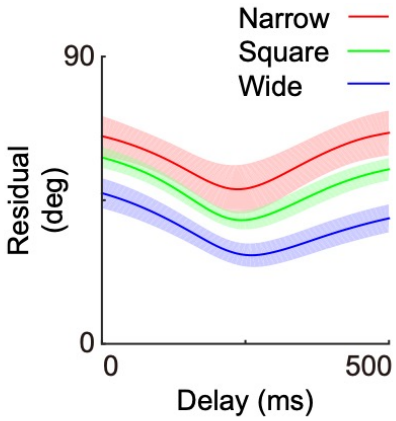

Figure 5-5 Fitness for the time-optimal model in each delay

The residuals between the observed and the predicted chase angle by the time-optimal model in each tau and in each condition. The red, green, and blue line indicate the narrow, square, and wide condition, respectively.

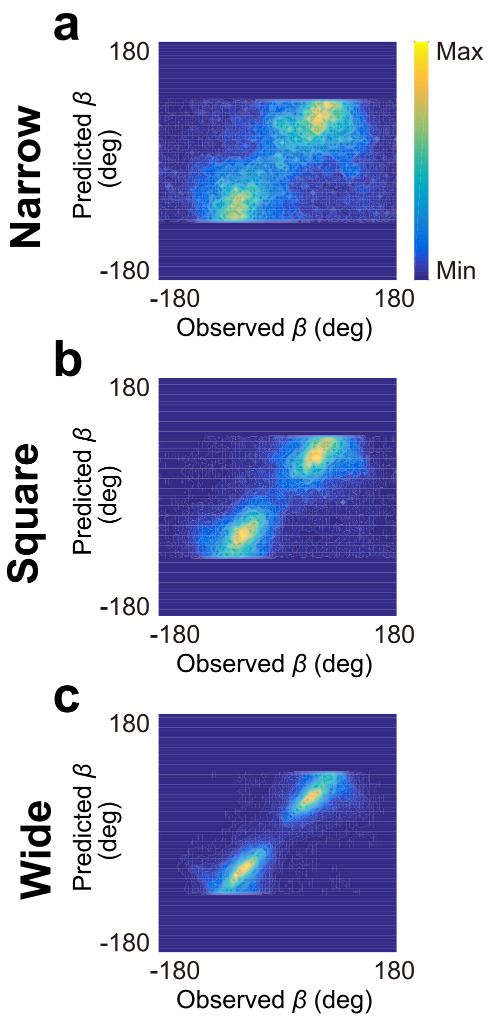

Figure 5-6 Fitness of the time-optimal model

(a-c) The contour map of the chase angles between observation and time-optimal model prediction of all data in (a) the narrow condition, (b) in the square condition, and (c) in the wide condition. The correlation coefficients ρ were 0.43 ± 0.16 in the narrow condition, 0.59 ± 0.09 in the square condition, and 0.74 ± 0.07 in the wide condition.

To examine the movement direction (i.e., chase angle) of the defender in more detail, I divided the whole trial into the initial phase and the other phase. Figure 5-7 shows the circular histograms in each phase and in each condition. This result indicated that the defender moved more straightly towards the attacker, compared to the time-optimal model, in the initial phase (like the classical pursuit).

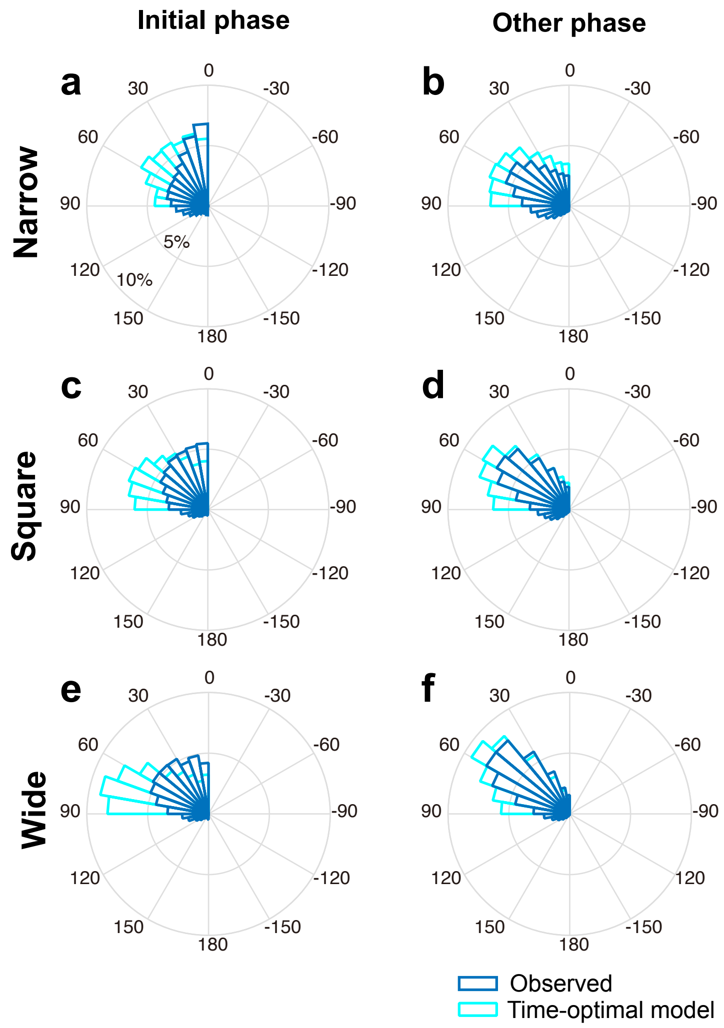

Figure 5-7 Distribution of chase angle in each phase

(a, c, e) The distribution of observed chase angle (blue) and predicted chase angle by the time-optimal model (cyan) in the initial phase (a) in the narrow condition, (c) in the square condition, and (e) in the wide condition. (b, d, f) The distribution of observed chase angle and predicted chase angle by the time-optimal model in the other phase (b) in the narrow condition, (d) in the square condition, and (f) in the wide condition.

Next, I examined the response time in more detail. The observed mean response time was 220 ± 18, 233 ± 24, and 248 ± 18 ms in each condition, and there were statistically significant differences among conditions (Figure 5-8; $F_{2, 22} = 20.4$, $\eta^2 = 0.26$, *ps* < 0.05, *ds* > 0.62). The shape of histogram in response time was similar among conditions (Figure 5-9), but the proportion of the predictive response (less than 200 ms) was greater as the width of court become narrower (Figure 5-10; $F_{2, 22} = 17.4$, $\eta^2 = 0.43$, *ps* < 0.05, *ds* > 0.96). A one-way repeated measured ANOVA revealed the main effect of the condition (Figure 5-11; $F_{2, 22} = 17.0$, $\eta^2 = 0.24$, *ps* < 0.05, *ds* > 0.60), and there were not significant effects in the positions of court (columns) and interaction. These results indicated that the difference in mean response time was a global feature rather than local, such as at the both side ends of the court (see Figure 5-3b, d, and f, again).

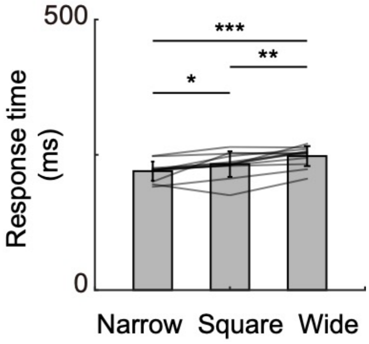

Figure 5-8 Mean response time

The observed mean response time was 220 ± 18 ms in the narrow condition, 233 ± 24 ms in the square condition, and 248 ± 18 ms in the wide condition. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

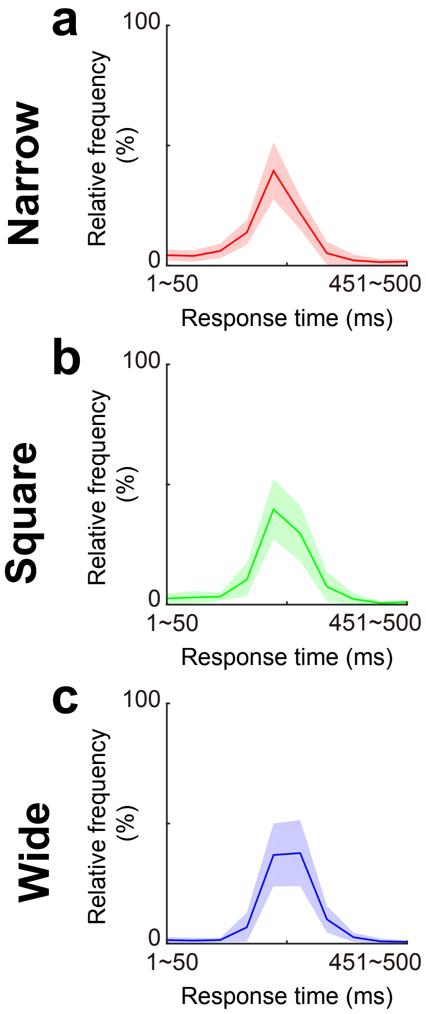

Figure 5-9 Histogram of response time

(a-c) The histogram of the observed response time (a) in the narrow condition, (b) in the square condition, and (c) in the wide condition. The width of each bin was set to 50 ms.

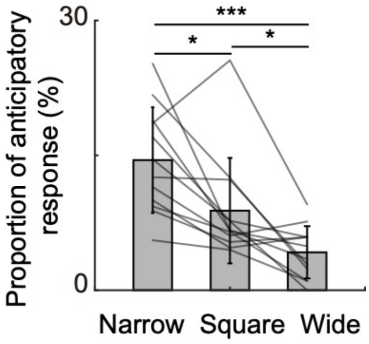

Figure 5-10 Proportion of predictive response

The proportions of predictive response (less than 200 ms) were 0.14 ± 0.06 ms in the narrow condition, 0.09 ± 0.06 ms in the square condition, and 0.04 ± 0.03 ms in the wide condition. *$p < 0.05$; ***$p < 0.001$.

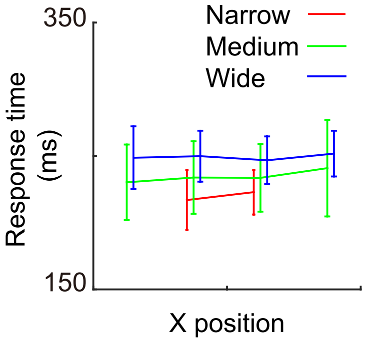

Figure 5-11 Mean response time in each *X* position

The mean response time in each *X* position. The red, green, and blue lines indicate the narrow, square, and wide condition, respectively. The width of each *X* position was set to half of the width of court in the narrow condition. Both two side ends of the *X* position in the wide condition are not shown because those contained missing values.

Experiment 6

In Experiment 6, I gave time constraints on the defender. Figure 5-12 shows the proportion of successful attack among conditions. The proportions of successful attack were 0.49 ± 0.10 in the short condition, 0.37 ± 0.14 in the long condition, and 0.34 ± 0.14

in the no-limit condition. A one-way repeated measured ANOVA revealed the main effect of the condition ($F_{1.45,\ 15.98} = 11.3$, $\eta^2 = 0.22$, $ps < 0.01$), and post hoc analysis revealed the proportion of successful attack in the short condition was higher than the other conditions (ps < 0.05, $ds > 0.98$).

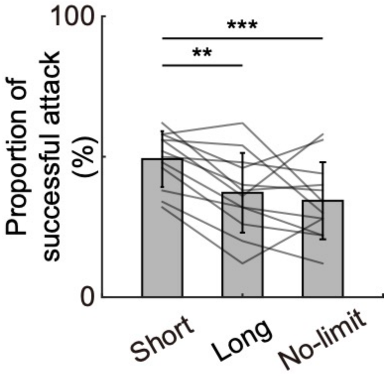

Figure 5-12 Proportion of successful attack

The proportions of successful attack were 0.49 ± 0.10 in the short condition, 0.37 ± 0.14 in the long condition, and 0.34 ± 0.14 in the no-limit condition. $^{**}p < 0.01$; $^{***}p < 0.001$.

Figure 5-13 shows the heat map of the position of the attacker, the that of the direction change, and the relative frequency, in each condition. The shorter the temporal constraints on the defender, the lower the frequency of reaching close to the end line (Figures 5-13a, d, and g), and it indicates that the attacker may have focused on using up the time limit rather than reaching the end line in time. In addition, the relative frequency of direction change of the attacker was approximately uniform in the court in each condition (Figures 5-13c, f, and i).

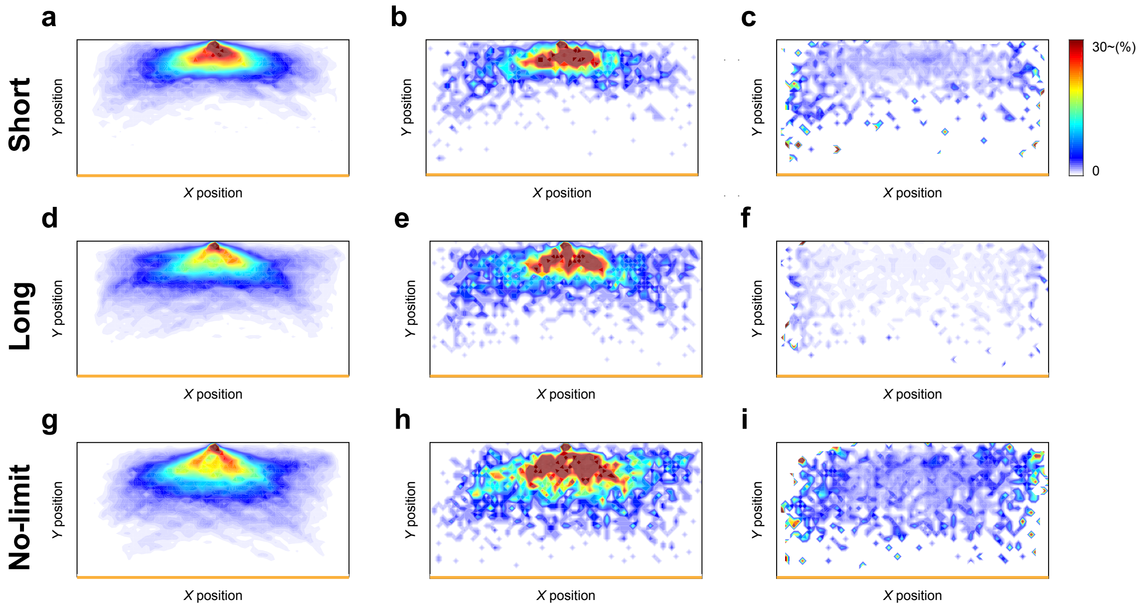

Figure 5-13 Heat maps regarding attacker

(a, d, g) 2D-histograms of time spent of the attacker in each position (a) in the short condition, (d) in the long condition, and (g) in the no-limit condition. (b, e, h) 2D-histograms of direction change of the attacker in each position (b) in the short condition, (e) in the long condition, and (h) in the no-limit condition. (c, f, i) The relative frequency of direction changes per time in each position (c) in the short condition, (f) in the long condition, and (i) in the no-limit condition. The court was divided into the cells of 20 square pixels each.

Then, I showed the heat map of the position of the defender and that of the response time, in each condition (Figure 5-14), the residuals in each tau and in each condition (Figure 5-15), and the heat map between the chase angles (Figure 5-16). There were no statistically significant differences among conditions in the residuals (Figure 5-15; $F_{2,\,22} = 0.26$, $\eta^2 = 0.008$, $p > 0.05$), and in the estimated visuo-motor delay (Figure 5-15; $F_{2,\,22} = 1.34$, $\eta^2 = 0.017$, $p > 0.05$). There were significant correlations between the observed and the predicted chase angle (Figure 5-16; 0.77 ± 0.06 in the short condition, 0.76 ± 0.07 in the long condition, and 0.78 ± 0.04 in the no-limit condition). These results indicate that the behavioral change of the defender was small among conditions.

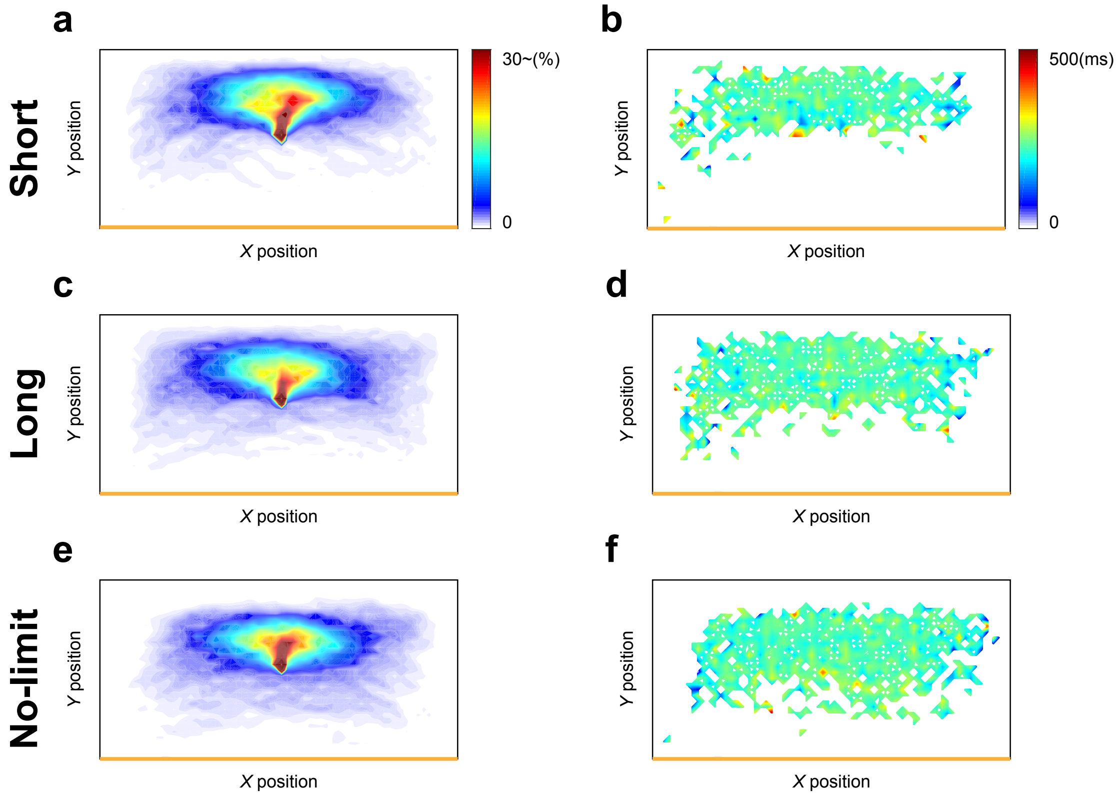

Figure 5-14 Heat maps regarding defender

(a, c, e) The 2D-histograms of time spent of the defender in each position (a) in the short condition, (c) in the long condition, and (e) in the no-limit condition. (b, d, f) The mean response times of the defender in each position (b) in the short condition, (d) in the long condition, and (f) in the no-limit condition. The court was divided into the cells of 20 square pixels each.

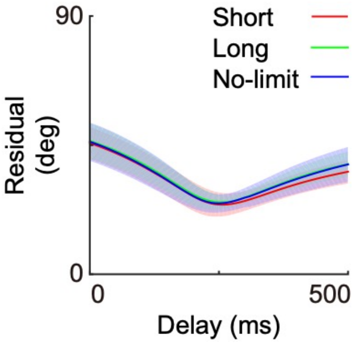

Figure 5-15 Fitness for the time-optimal model in each delay

The residuals between the observed and the predicted chase angle by the time-optimal model, in each tau and in each condition. The red, green, and blue line indicate the short, long, and no-limit condition, respectively. There were no statistically significant differences among conditions.

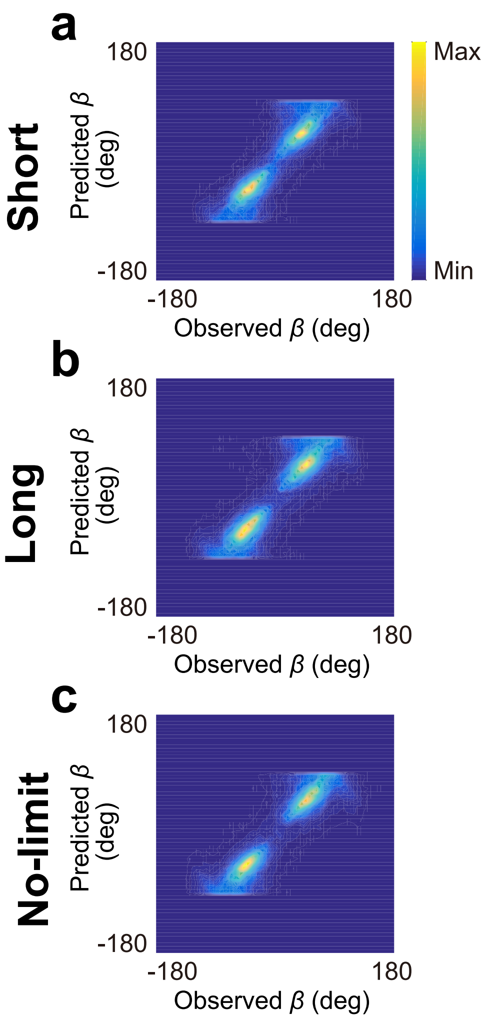

Figure 5-16 Fitness for the time-optimal model

(a-c) Contour map of the chase angles between observation and time-optimal model prediction of all data in (a) short, (b) long, and (c) no-limit condition. The correlation coefficients ρ were 0.77 ± 0.06 in the short condition, 0.76 ± 0.07 in the long condition, and 0.78 ± 0.04 in the no-limit condition

Then, I examined the behavioral change of the attacker. Figure 5-17 shows the scatter plots of the successful attack (red circle) and defense (dark blue cross). This shows that, many successful attacks were achieved due to the time restriction in the short condition. These results indicated that the attacker tended to put the weight on escape rather than penetrate as the time restriction on the defender was severe. Thus, I compared the escape angle of attacker between conditions (Figures 5-18 and 19). A one-way repeated measured ANOVA revealed the main effect of the condition (Figure 5-19; $F_{2, 22} = 7.1$, $\eta^2 = 0.22$, $p < 0.01$), and post hoc analysis revealed the attacker's escape angle in the short condition was greater than the no-limit condition ($p < 0.01$, $d = 1.1$). These results indicate that the movement directions of the attacker relative to the defender were distributed in a direction closer to 180 degrees as the temporal constraint becomes severe.

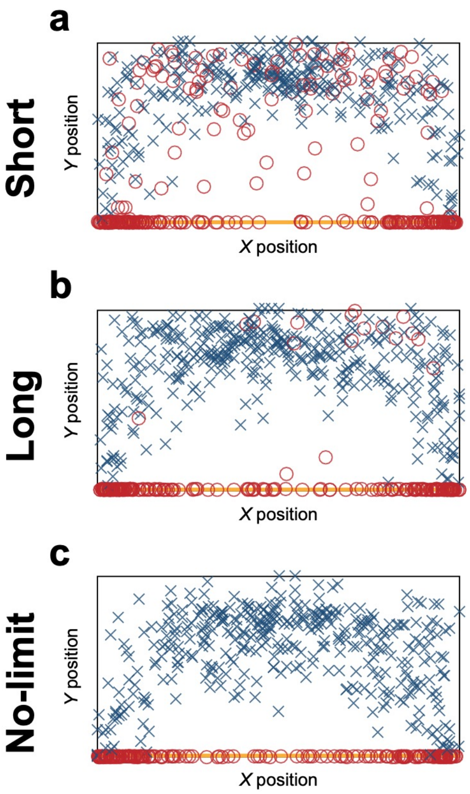

Figure 5-17 Scatter plots of successful attack and defense

(a-c) The scatter plots of successful attack (red circle) and defense (blue cross) (a) in the short condition, (b) in the long condition, and (c) in the no-limit condition. Many successful attacks were distributed over a wide area on the court in the short condition.

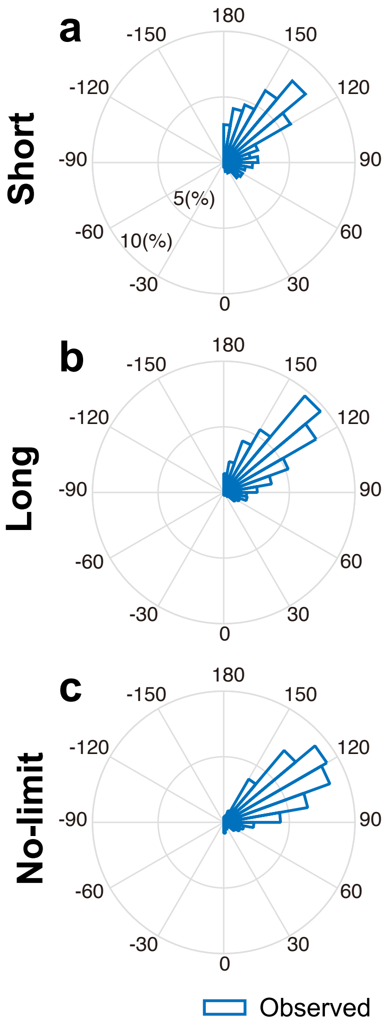

Figure 5-18 Distribution of escape angle

(a-c) The distribution of observed chase angle (a) in the short condition, (b) in the long condition, and (c) in the no-limit condition. The angles of negative value were reversed to those of positive value. The width of each bin was set to 10 degrees.

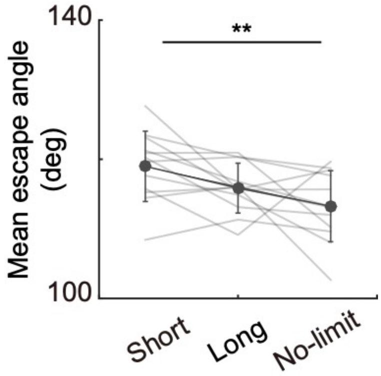

Figure 5-19 Mean escape angle

The mean escape angles were 119 ± 5.0 in the short condition, 116 ± 3.6 in the long condition, and 113 ± 5.1 in the no-limit condition. $^{**}p < 0.01$.

In addition, I investigated the change of the decisions of the attacker. In this analysis, we computed the theoretically penetrable opportunity in each trial (Figure 5-20), and we compared it with the number of actual penetrations (Figure 5-21). Note that the actual number of penetrations refers to the number of reaching the end line without being caught by the defender and does not refer to the unsuccessful attack. A one-way repeated measured ANOVA revealed the main effect of the condition (Figure 5-22; $F_{2,22} = 9.6$, $\eta^2 = 0.28$, $p < 0.01$), and post hoc analysis revealed the proportion of the actual penetrations to the theoretically penetrable opportunities in the short condition was lower than the other conditions ($ps < 0.05$, $ds > 1.1$).

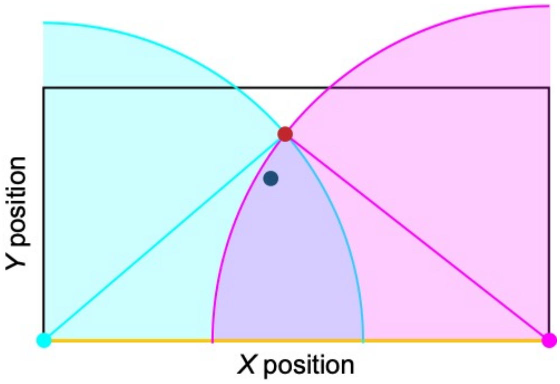

Figure 5-20 Theoretically penetrable opportunity

The cyan circle shows the distance from the lower left corner of the court to the attacker, and the magenta circle shows the distance from the lower right corner of the court to the attacker. If the distance from one of the corners to the defender is greater than the distance from the corner to the attacker, the attacker can theoretically reach the end line without be caught by the defender. That is, if the defender leaves the purple area (the overlapping area of cyan and magenta), the attacker can theoretically win.

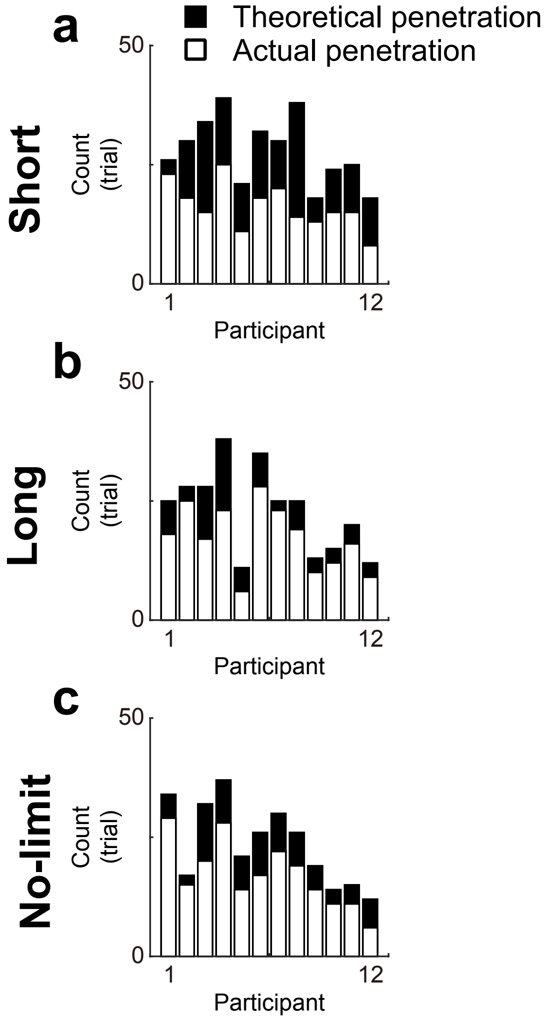

Figure 5-21 Comparison between theoretical and actual penetration

(a-c) Comparisons between the number of theoretically penetrable trial (black bar) and that of actually penetrated trial (white bar) (a) in the short condition, (b) in the long condition, and (c) in the no-limit condition, in each participant.

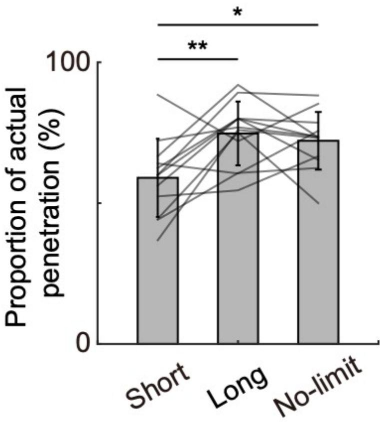

Figure 5-22 Proportion of actual penetration

The proportions of actual penetration were 0.59 ± 0.14 in the short condition, 0.75 ± 0.11 in the long condition, and 0.72 ± 0.10 in the no-limit condition. $*p < 0.05$; $**p < 0.01$.

Experiment 7

In Experiment 7, I gave time constraints on the attacker, and the analysis was conducted as in Experiment 6. Figure 5-23 shows the proportion of successful attack among conditions. The proportions of successful attack were 0.33 ± 0.14 in the narrow condition, 0.37 ± 0.20 in the square condition, and 0.33 ± 0.18 in the wide condition. There was no statistically significant difference between conditions ($F_{2,22} = 0.96$, $\eta^2 = 0.012, p > 0.05$).

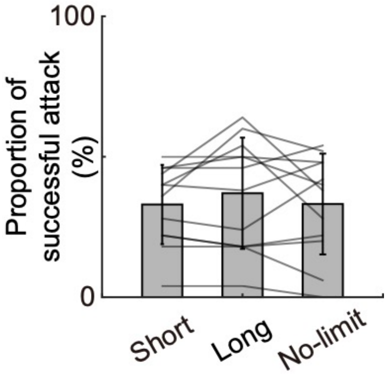

Figure 5-23 Proportion of successful attack

The proportions of successful attack were 0.33 ± 0.14 in the narrow condition, 0.37 ± 0.20 in the square condition, and 0.33 ± 0.18 in the wide condition.

Figure 5-24 shows the heat map of the position of the attacker, the that of the direction change, and the relative frequency, in each condition. This result indicates that the spatial characteristics regarding direction changes of the attacker was small among conditions.

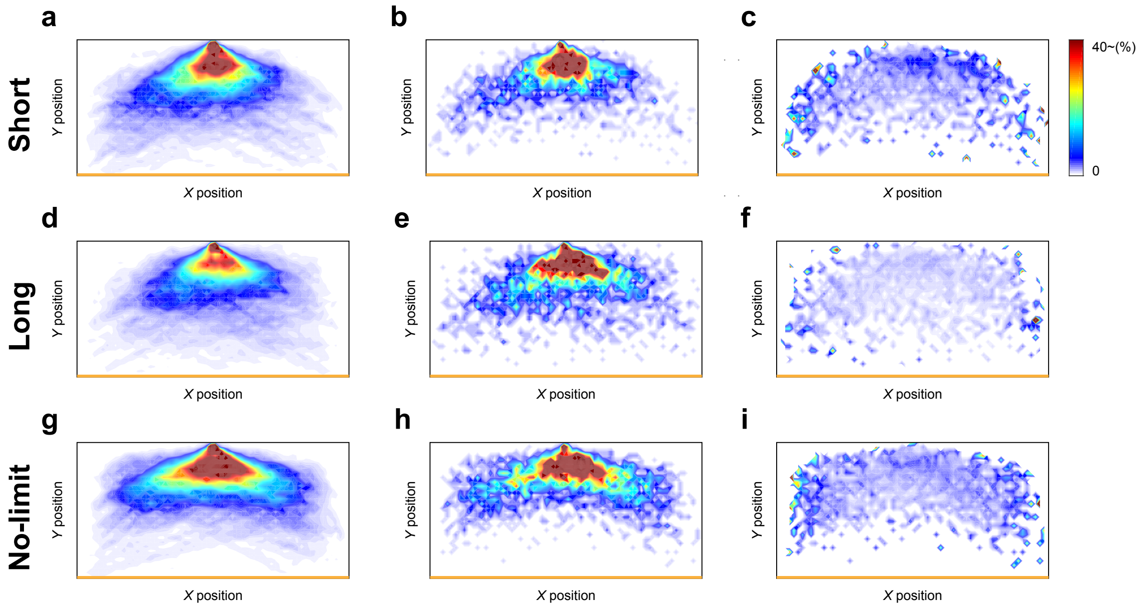

Figure 5-24 Heat maps regarding attacker

(a, d, g) The 2D-histograms of time spent of the attacker in each position (a) in the short condition, (d) in the long condition, and (g) in the no-limit condition. (b, e, h) The 2D-histograms of direction change of the attacker in each position (b) in the short condition, (e) in the long condition, and (h) in the no-limit condition. (c, f, i) The relative frequency of direction changes per time in each position (c) in the short condition, (f) in the long condition, and (i) in the no-limit condition. The court was divided into the cells of 20 square pixels each.

Figure 5-25 shows the heat map of the position of the defender and that of the response time, in each condition. Figure 5-26 shows the residual and the correlation coefficient between the chase angles in each delay. There were no statistically significant differences among conditions in the residual (Figure 5-26; $F_{2, 22} = 1.12$, $\eta^2 = 0.024$, $p > 0.05$) and in the estimated visuo-motor delay (Figure 5-26; $F_{2, 22} = 0.74$, $\eta^2 = 0.011$, $p > 0.05$). Figure 5-27 shows the relationship between the observed chase angle and the predicted chase angle by the time-optimal model, and there were statistically significant correlations (0.72 ± 0.07 in the short condition, 0.74 ± 0.08 in the long condition, and 0.75 ± 0.10 in the no-limit condition). These results indicate that the behavioral change of the defender was small among conditions.

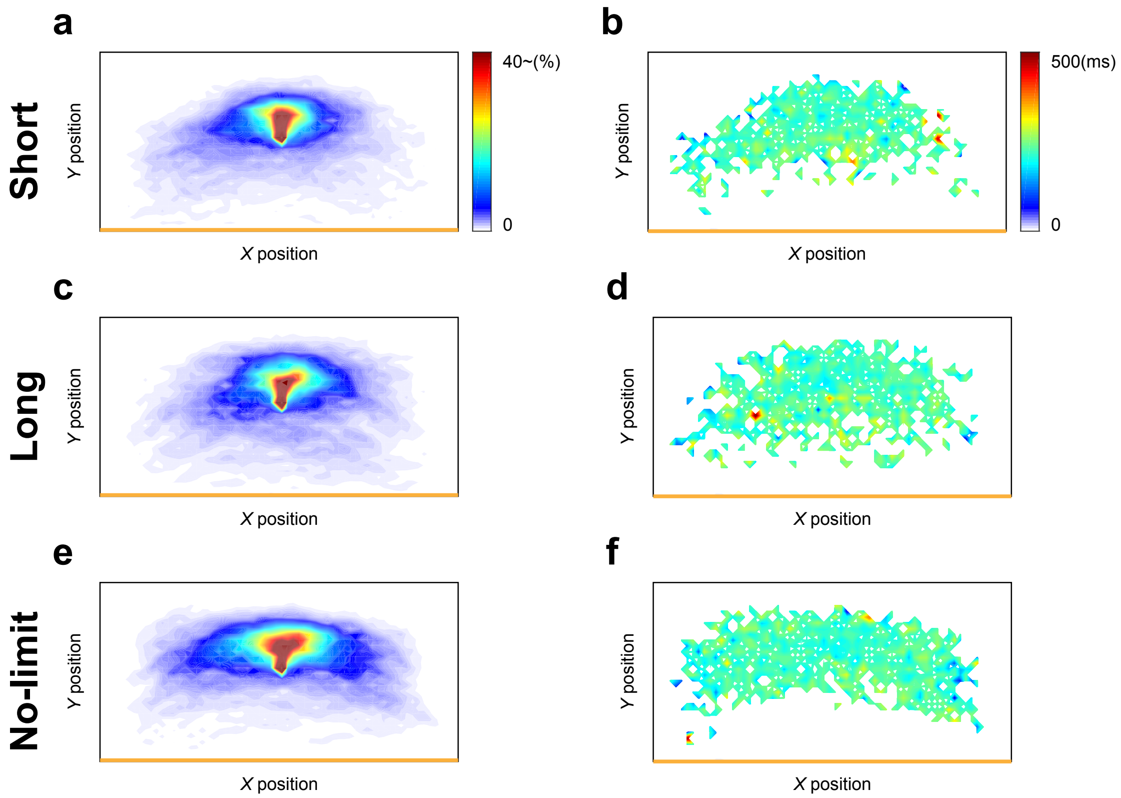

Figure 5-25 Heat maps regarding defender

(a, c, e) The 2D-histograms of time spent of the defender in each position (a) in the short condition, (c) in the long condition, and (e) in the no-limit condition. (b, d, f) The mean response times of the defender in each position (b) in the short condition, (d) in the long condition, and (f) in the no-limit condition. The court was divided into the cells of 20 square pixels each.

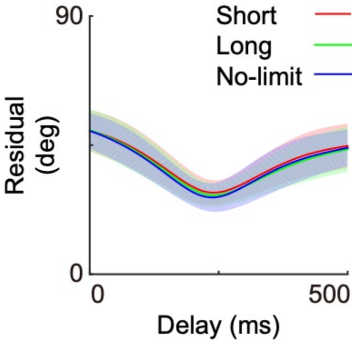

Figure 5-26 Fitness for the time-optimal model in each delay

The residuals between the observed and the predicted chase angle by the time-optimal model in each tau and in each condition. The red, green, and blue line indicate the short, long, and no-limit condition, respectively.

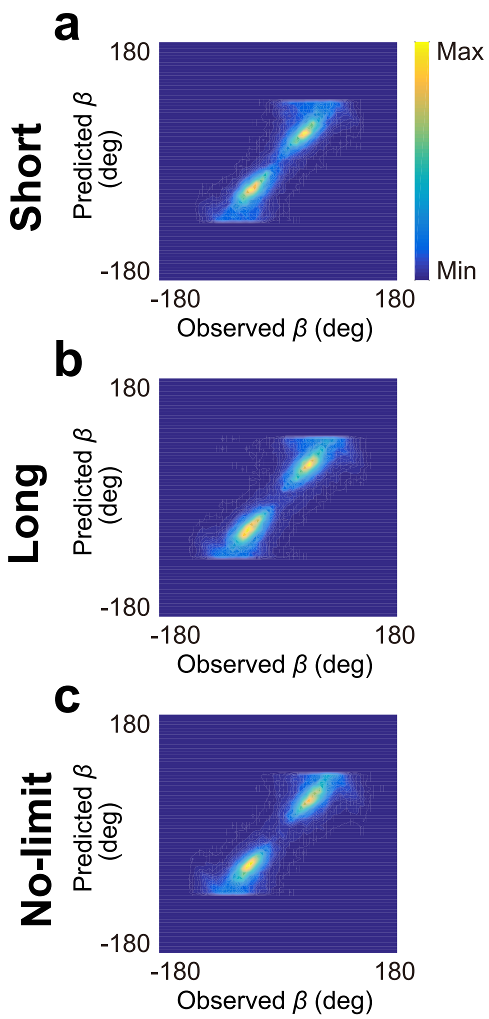

Figure 5-27 Fitness for the time-optimal model

(a-c) The contour map of the chase angles between observation and time-optimal model prediction of all data (a) in the short condition, (b) in the long condition, and (c) in the no-limit condition. The width of each cell was set to 5 degrees.

Figure 5-28 shows the histograms of the escape angles. A one-way repeated measured ANOVA revealed the main effect of the condition (Figure 5-29; $F_{2,22} = 5.5$, $\eta^2 = 0.16$, $p < 0.05$), and post hoc analysis revealed the attack's escape angle in the short condition was smaller than the no-limit condition ($p < 0.05$, $d = 1.1$). The proportion of the proportion of the actual penetrations to the theoretically penetrable opportunities was not significantly different among conditions (Figures 5-30 and 31; $F_{1.42,\ 15.61} = 1.8$, $\eta^2 = 0.056$, $p > 0.05$).

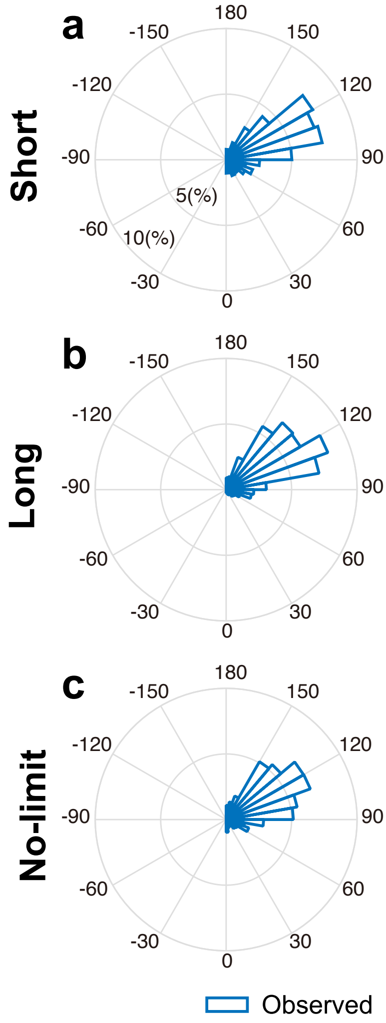

Figure 5-28 Distribution of escape angle

(a, b, c) The distribution of observed chase angle (a) in the short condition, (b) in the long condition, and (e) in the no-limit condition. The angles of negative value were reversed to those of positive value. The width of each bin was set to 10 degrees.

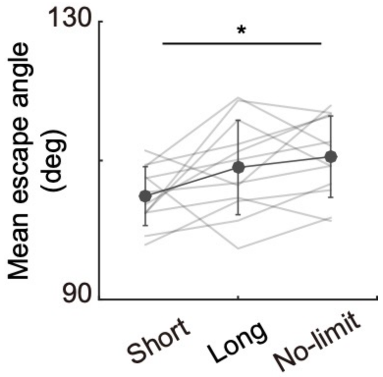

Figure 5-29 Mean escape angle

The mean escape angles were 105 ± 4.2 in the short condition, 109 ± 6.8 in the long condition, and 111 ± 5.9 in the no-limit condition. There was statistically significant difference between short and no-limit conditions. *$p < 0.05$.

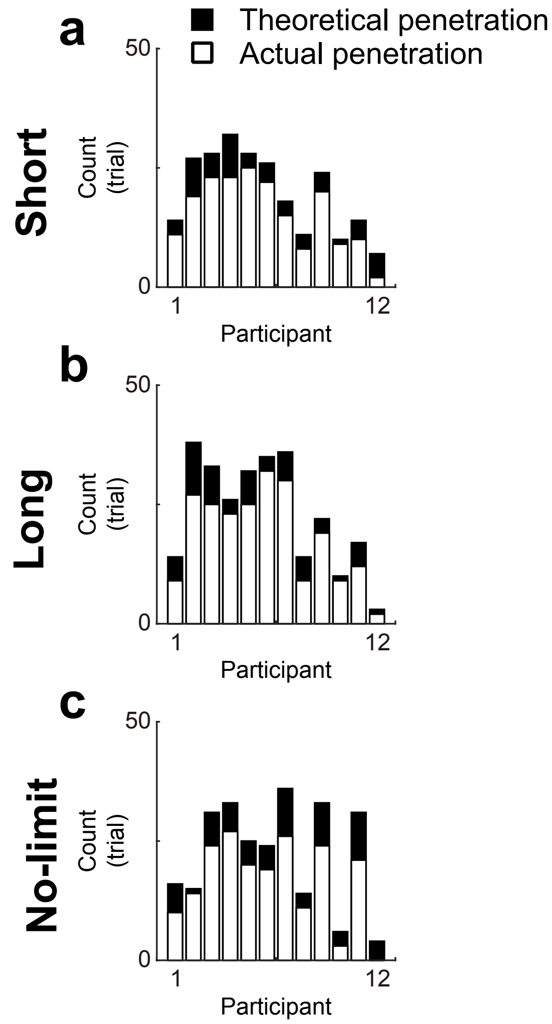

Figure 5-30 Comparison between theoretical and actual penetration

(a-c) Comparisons between the number of theoretically penetrable trial (black bar) and that of actually penetrated (i.e., reached the end line) trial (white bar) (a) in the short condition, (b) in the long condition, and (c) in the no-limit condition, in each participant.

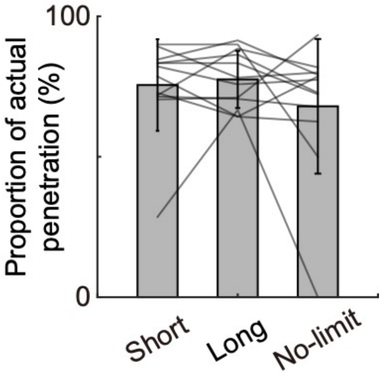

Figure 5-31 Proportion of actual penetration

The proportions of actual penetration were 0.76 ± 0.16 in the short condition, 0.78 ± 0.10 in the long condition, and 0.68 ± 0.24 in the no-limit condition. There were no statistically significant differences among conditions. *$p < 0.05$; **$p < 0.01$.

5.4 Discussion

In this study, I examined the effects of environmental constraints on the behaviors and the outcomes for human chase-and-escape interactions. There were some changes in behaviors (or strategies) of the agents corresponding to the environmental constraints, the overall results were consistent with the results of Studies 1 to 3. As a result, the behavioral outcomes greatly depended on the environmental constraints (i.e., experimental conditions).

The chase angle of the defender was approximately consistent with the time-optimal model in the wide condition. On the other hand, the chase angle was less consistent with the time-optimal model in conditions where the spatial constraint was severe. In addition, in the initial phase, the chase angle concentrated on near zero degrees. These results suggest that pursuers can change their strategies flexibly according to environments while they are based on the time optimal strategy.

The response time shortened as the spatial constraints became more severe. The shape of histograms was similar among conditions, whereas the proportion of predictive responses was greater as the width of court become narrower. These results suggest that the shortness of mean response time is related to the predictive responses. Moreover, in the analyses of mean response time in each position of the court, the response time decreased globally rather than locally. In other words, the response time decreased for the entire court rather than for both edges of the court. This result suggests that the restrictions of escape behavioral pattern, rather than position coordinates of the evader, facilitate predictive response to the pursuer.

Whereas severe time constraints (i.e., the short condition) to the defender increased the attack success rate, there was no statistically significant difference in attack success rate between the loose time constraint (the long condition) and no time constraint (the no-limit condition) to the defender (see Figures 12 and 23). As shown in Figure 17, in the long condition, there were not many successful attacks due to the time restriction, and it might be easier to reach the end line (penetration) than to wait for the passage of time in the court. The results of the proportion of the actual penetration number to the theoretically possible penetration number indicates that the attackers tended to escape rather than to penetrate in the short condition compared with the long and no-limit conditions. These results suggest that escape behavior and its decision-making could change depending on time constraints. In addition, the proportion of the actual penetration to the theoretically possible penetration was about 70-80% even in the conditions where there was no time limit or the attacker temporally constrained (see Figures 5-22 and 5-31). These results provide the insight that it would be difficult to detect opportunities and try to penetrate properly in chase-and-escape interactions where situations change quickly and continuously.

The movement direction of the attacker relative to the defender changed due to time constraints. That is, the absolute escape angle increased (near 180 degrees) in the time constraint on the defender, whereas the absolute escape angle decreased (near 90 degrees) in the time constraint on the attacker. These results indicated that the weights on the two requirements, namely avoiding being caught and reaching the end line (see Study 3 for detail), were changed according to time constraints in order to meet these requirements simultaneously, and it suggests that the attackers fine-tuned their movement directions (i.e., escape angle) according to the temporal constraints.

On the other hands, the movement direction of the defender (chase angle) did not change due to time constraints on both the defender and the attacker. Given that the defender adopts the time-optimal strategy, it would be reasonable that the strategy did not change due to the time constraints on the defender. However, the strategy also did not change under the time constraints on the attacker. In conditions where the attacker is limited its movement time, the attacker should try to reach the end line more straightly. As a result, the defender did not necessarily have to move to the attacker's side. That is, it would be possible to achieve defense success with only lateral movement in the absolute coordinate systems, such as side steps. However, the defender in fact did not use such strategy. It might be because the time-optimal strategy is effective in terms of increasing the capture success rate.

5.5 Summary

In summary, the pursuer and evader flexibly change their behaviors to accomplish the objectives, but the degree of change is relatively small and the outcomes greatly depended on the environmental constraints. These results suggest that, in addition to the parameters of the agents shown in Study 3, environments surrounding the agents would also be a crucial determinant of the behavioral outcomes.

Chapter 6

General discussion

6.1 Summary of the present studies

Here, I summarize the results of the present studies in the form of answers to each research question raised in Chapter 1.

Chase strategy: How do humans intercept a fleeing target? Also, is there a difference in the strategy between agents who are good at interception and those who are not?

In Study 1 (Chapter 2), I investigated the chase strategy of purser (defender) in chase-and-escape interactions through mathematical modeling of actual interactive human behaviors using two chase-and-escape tasks in real space (Experiment 1) and in virtual space (Experiment 2). In both experiments, the pursuer's behavior was well reproduced by the time-optimal model. In addition, this result was approximately consistent between agents who are good at interception and those who are not. These suggest that humans use the time-optimal strategy for intercepting a fleeing target in chase-and-escape interactions.

Escape strategy: How does evader reach to a safety zone behind an opponent? Also, are there some characteristics for the direction change of the evader (attacker) and response to it of the pursuer (defender).

In Study 3 (Chapter 4), I investigated the evasive strategy of the attacker regarding movement direction. The results showed the attackers largely moved at an obtuse angle (away direction) with respect to the position of the defender, and, by tilting their positional relationship (i.e., bearing angle), met the two requirement (i) to avoid being caught by the defender and (ii) to reach the end line behind the defender. In addition, in Study 2 (Chapter 3), I investigated the evasive strategy of the attacker regarding direction change. In this study, I focused on the probability distribution regarding direction changes of the attacker and the response times to those of the defender in chase-and-escape interactions. The results showed that the attacker's direction change has two characteristics: uniformity of spatial distribution and bimodality of temporal distribution, and these suggest that the evader could combine the unpredictability to prevent the defender's predictive response and the effectiveness to obtain the benefit of an extra response delay of tens of milliseconds, in its change of directions.

Determinants of chase-and-escape outcomes: Does manipulation of a parameter directly change the outcomes of their interactions? Or are adaptive behavioral changes observed corresponding such parameter manipulations?

In Study 3 (Chapter 4), in order to investigate the determinants of the chase-and-escape outcomes, I reanalyzed the data of Experiment 3 and conducted another chase-and-escape task (Experiment 4). The compensatory movements of individual agent corresponding to the manipulation of the parameter (i.e., movement speeds in Experiment 3 and response time in Experiment 4) was small in the range of manipulation in this study (at least not enough to compensate the manipulation of the parameter), and thus the outcome of agents' behaviors is substantially dependent on their parameters of maneuverability.

Behavioral changes due to environmental constraints: Do spatiotemporal constraints, which is major in sports, change human chase and/or escape behaviors? If so, what and how do those change?

In Study 4 (Chapter 5), in order to investigate the effects of the environmental constraints on their behaviors and the outcomes (successful interception or escape), three chase-and-escape tasks manipulated spatial constraint (Experiment 5) and given temporal constraints on defender (Experiment 6) and on attacker (Experiment 7) were performed. The result showed the spatial and temporal constraints affected the chase and escape strategies, but the change of their strategies is small, in the range of manipulation in this study. As a result, the outcome of agents' behaviors is substantially dependent on the spatiotemporal constraints.

6.2 Behavioral rules

In this thesis, I investigated the chase strategy, the escape strategy, the determinants of the outcome, and the effects of the environmental constraints, in human chase-and-escape behaviors. Although there seems to be individual differences in the strategy because there are a lot of freedom of movement in the chase-and-escape tasks, interestingly each result was consistent among participants throughout the studies. Here, I discuss the reason why some rules exist in spite of complex interactions, based on the results gained by my studies from the perspective of chase behaviors and escape behaviors, respectively, below.

6.2.1 Chase behavior

6.2.1.1 Movement direction

In this thesis, I investigated the human chase strategy in the chase-and-escape interactions by applying the mathematical models proposed in biology. Through the studies, human chase behaviors were approximately reproduced by the time-optimal model, though the deviations increased due to severe spatial constraints. This indicates that humans move based on the time-optimal strategy to capture a fleeing target, and this suggests that the human chase strategy is in common with other many animals rather than a human-specific. There are several advantages (or biological plausibility) of using the time-optimal strategy. Firstly, the strategy provides the local shortest path, and it would be effective for intercepting a moving target. Secondly, the time-optimal model depends only on positions and velocities to determine the movement direction (see Equation 2). In other words, it does not require information on acceleration (Bootsma, Ledouit, Casanova, & Zaal, 2016; Dessing & Craig, 2010) or a time window to integrate sensory information (Bar, Skogestad, Marçal, Ulanovsky, & Yovel, 2015). The simplicity of the computation can contribute to reducing the processing load in the brain and may allow pursuer to determine quickly the movement direction. Finally, this strategy determines the movement direction at the next moment based on the target direction at a certain moment so that the direction does not change. Such nullifying strategy are known to be robust against perceptual errors and disturbances (McBeath et al., 1995) and may be suitable for chase behaviors that require quick and accurate sensorimotor control in environments with a lot of disturbances (e.g., ground irregularities or sudden winds). Considering these advantages, the adoption of the time-optimal strategy is one of the rational means to capture a target, and it may be associated with the commonality in chase strategy in a variety of animal species ranging from fish, amphibians, birds to humans.

6.2.1.2 Response to direction change

Although the previous studies on non-human chase behaviors have assumed purely reactive controls, the pursuer in my study sometimes responded predictively to the direction change of evader, in particular when the spatial constraint was severe. In the previous studies on chase behaviors in non-human, it has been assumed that pursuers detect the position of the target and correct the movement direction with the visuo-motor delay. However, as shown in Study 4, the more severe the spatial constraints, the greater the proportion of predictive responses of the pursuer to the direction change of the evader, and this suggests that the pursuer can response predictively in situations where the behavior pattern of the evader is limited. As far, it has been reported that the prediction of direction change is performed by using the body kinematics information of the evader (attacker), but the result of this study indicates that it can be predicted only from the trajectory. In this connection, the reason of little predictive response in a weak spatial constrained situation in spite of having such predictive ability is probably that reckless predictive responses (i.e., incorrect prediction) will result in great losses of chance of the capture.

6.2.2 Escape behavior

6.2.2.1 Movement direction

In this thesis, I investigated the human escape strategy in the chase-and-escape tasks in which the attacker is required to reach the end line behind the defender. This is somewhat different from the chase-and-escape behaviors in nature in terms of whether the movement direction of the evader is limited or not. However, the escape angle, which is the movement direction of the evader (attacker) relative to the pursuer (defender) was distributed at obtuse angles. In addition, even when the spatial constraints were severe, the escape angles were similarly distributed in obtuse angles. This distribution of the escape angle in the obtuse angle is consistent with the findings of the escape behaviors in non-human animals (see Chapter 1-1-2), and these suggest that the movement away from the threat is rational for escape behaviors in broad situations. On the other hand, the multimodality of the escape angles, as observed in cockroaches (Domenici et al., 2008), was not observed in my studies. This is probably due to the task constraint, which required the attacker to reach the end line behind the opponent. In such situations, the attacker would not approach the opponent when the escape angle is within the range of 90 to 180 degrees. However, as the escape angle is closer to 180 degrees, the greater the inclination of the positional relationship is necessary to approach the end line. Considering such a geometrical relationship, the escape angle closer to 90 degrees should be more effective in achieving the task. In fact, the mean escape angle is close to 90 degrees under severe time constraints. These suggest that the evader can select (adjust) the escape angle within the range of 90 to 180 degrees, but the behavior is actually quite limited from the viewpoint of rational selection that satisfies the task constraints.

6.2.2.2 Direction change

As described above, the escape angle is approximately constant and it would be easy for the pursuer to predict the movement direction of the opponent, from the viewpoint of the defender. On the other hand, it would be difficult for the pursuer to predict the sudden direction change of the evader because the pursuer made the global probability (relative frequency per time) in the direction changes uniform on the court. Interestingly, this characteristic of spatially uniform distribution was consistent among participants, whereas temporal distribution was not consistent among participants. If the probability (or frequency) bias gives the opponent a clue of the prediction, the temporal distribution should be also as uniform as possible, at least in the direction changes with long-interval. Thus, these might indicate that the pursuer preferentially uses the spatial cues rather than the temporal one for the prediction of the direction change. Anyway, in the direction change of the evader, the constraints to make the probability distribution uniform in the spatial aspect would be strong, while there may be rooms of the choice in the temporal aspect. Also, to increase the unpredictability against the opponent in some way may be an important factor in competitive interactions because a single strategy (or fixed behavioral pattern) could leave an animal vulnerable to the opponent with the capability to exploit the strategy. For example, the redstart takes advantage of the escape response of the fly by flicking its tail to mimic looming stimuli, triggering the fly jump response. By this method, the redstart flushes flies their perches and then catches them in the air (Jablonski, 1999; Jabłoński & Strausfeld, 2000, 2001). Therefore, acquiring strategies that increase unpredictability may be rational in evolutionary and learning processes.

In summary, the agents in the chase and escape behaviors flexibly adjusted their behaviors according to aims of the agents, task constraints, and environmental constraints, but the selections of the behaviors are quite limited from the viewpoint of rationality. As a result, some rules would be formed among the complex interactions.

6.3 Future directions

In this thesis, I focused on overall rules of the agent behaviors and the outcomes, that is, the underlying structures, in human chase-and-escape behaviors. Although these analyses revealed some behavioral patterns and rules, there are still many unclear points. Therefore, I here show three future directions.

6.3.1 Sensory and motion interaction

One of the future directions is to incorporate the sensory and motor interactions. Locomotion in animals are constrained by a loop comprising their nervous system, musculoskeletal system, and external environment (Dickinson, 2000; Roth, Sponberg, & Cowan, 2014; Tytell, Holmes, & Cohen, 2011). Given this loop, mechanical constraints, which comprise the musculoskeletal system and the external environment, are critical for performing the chase and escape behaviors. Most of the studies in this thesis examined the chase-and-escape behaviors using virtual tasks, and there is no limit on the acceleration of the agent movements in the tasks. However, in actual locomotion, an animal needs to exert a force on the external environment to accelerate, and the acceleration is constrained by body mass and the ability of the musculoskeletal system to generate the force. Moreover, the horizontal force is limited by friction to avoid sliding, especially in turns with a small radius, in terrestrial locomotion (Tan & Wilson, 2011). As a result, it would be necessary to select a strategy that match own motor abilities in actual chase and escape behaviors. In fact, a study on the response behaviors of goalkeepers in penalty shootouts suggests that humans changes their strategies according to their motor abilities[10] (Dicks, Davids, & Button, 2010). In Chapter 1-1, I outlined the three dominant chase strategies of animals, and it should be noted that the third strategy, namely parallel navigation, have been observed in aerial animals such as dragonflies (Olberg et al., 2007, 2000; Olberg, 2012) and bats (Ghose et al., 2006). That is, they might have adopted the parallel navigation strategy as an alternative of the time-optimal strategy because it is difficult to obtain a large centripetal acceleration force in the air and thus they cannot move along the time-optimal path. Therefore, studies considering the interaction of sensory and motor abilities including morphological features within individual (or even between individuals) might explain the diversity in chase and escape strategies.

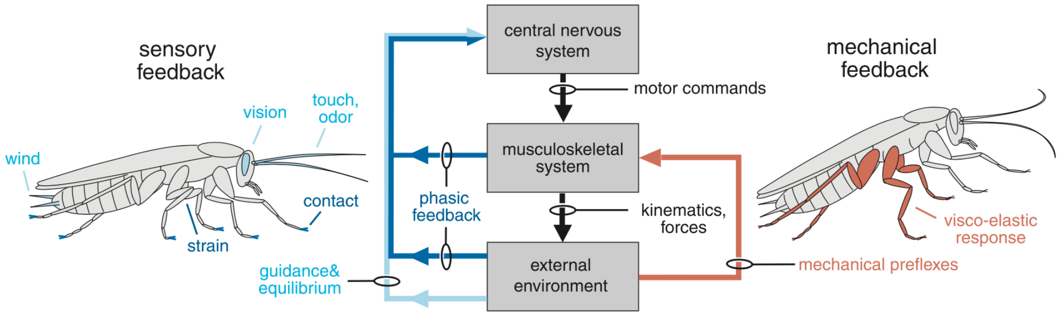

Figure 6-1 Sensory-motor loop

The diagram represents a general model for locomotor control. The central nervous system generates motor commands that activate the musculoskeletal system of the animal. The musculoskeletal system, in turn, acts on the external environment. The external environment is sensed by multiple modalities and fed back to the central nervous system. The nervous system processes the sensory feedback and modifies the motor commands. (Cited from Dickinson et al., 2000)

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[10] Specifically, in this study, the goalkeepers who can move quickly began later to move (greater response time) and the response is more accurately (higher proportion of correct response in direction), than the goalkeepers who cannot move quickly.

6.3.2 Time series structure

Another of future directions is to investigate the chase-and-escape behaviors in more detail. For example, in Study 1, I showed that deviations between observed chase angle and the time-optimal model prediction were greater in the turning phase, but the reason and details are not clear. One reason of this great deviation is thought to be a variation in reaction time, but there may be other reasons. One possibility is a temporary intentional deviation from the time-optimal path. Specifically, when the response to the direction change of the attacker is delayed, once defenders may place more emphasis on not being passed than catch in order to recover the situation. In addition, in Study 2, I showed that the attacker increased a spatial uniformity regarding the distribution of direction changes to prevent the defender from prediction, but the process is unknown. That is, there may be local rules in time series changes, and the defender might be able to predict the direction changes of the attacker using the local rules. Or the attacker might randomize its behaviors to remove even such local rules. These more detailed analyses considering the time series may provide the insight that sophisticated cognitive processes such as flexible strategic changes in context and psychological recursion with others.

6.3.3 Group chase and escape behavior

The last future direction is to expand the scope of chase-and-escape behaviors to more agents. In this thesis, I focused on one-on-one chase-and-escape behaviors, but chase-and-escape behaviors is not necessarily one-on-one. In nature, there are many animals that form groups on both predators and prey. In particular in social animals, many cooperative behaviors that improve the benefits of the entire group such as the sharing of knowledge and foods have been observed. For example, vampire bats, *Desmodus* *rotundus*, distribute foods (i.e., blood) among individuals and it is considered that the food distribution increase the chances of survival of each individual (Carter & Wilkinson, 2013). Also, the advantage of evaders to form groups has been reported in the interactions between frogs (prey) and snake (predator). These findings suggest that group behaviors can benefit the individual who forms the group. However, the number of studies is limited because it is difficult to observe repeatedly these behaviors even in the experimental environment as well as in nature, and there are many unclear points. Although a few studies have investigated the group chase and escape behaviors using computer simulations, the movement rules of chasers and targets are unrealistic (Kamimura & Ohira, 2010; Nishi, Kamimura, Nishinari, & Ohira, 2012; Saito, Nakamura, & Ohira, 2016). Thus, it would be necessary to investigate the group chase and escape behaviors in a way that extends the findings of the one-on-one chase and escape behavior. One of the leading subjects for understanding group chase-and-escape behaviors is the sports, such as football, rugby, and basketball because these sports is ease to observe and previous research including my studies has accumulated a lot of findings. The competitive interaction between these multi agents seems complex, but there should also be some rules formed by the constraints of rational choice. For example, the division of defensive space among agents are often observed in actual games (called "zone defense"), and this may be beneficial from the results of Study 5. Therefore, the multi agent sports may be useful to investigate human group chase-and-escape behaviors, and these findings may provide insights into the collective behaviors (or intelligence) of animals.

6.4 Implications for sports

I here mentioned two implications based on the findings obtained in my studies. The first is tactics and guidance from the viewpoint of movement speed and response delay, and the second is the importance of movements without a ball from the perspective of agent behavior being constrained. However, it should be noted that these findings were mainly obtained in the chase-and-escape task in the virtual space, and that careful discussion is required when applying them to actual sports and instructions.

6.4.1 Relation between speed and delay

In Study 3, I showed that the success rate of attack and defense is roughly determined by the relationship between movement speed and response (or visuo-motor) delay. Note that, the maximum movement speeds of the two agents are equal in these experiments (Experiment 3 and 4). In particular, the difference between speed conditions in Experiment 3 is the absolute (not relative) movement speed of the agent and it is considered to correspond to the children and adults or the male and female in sports. This is consistent with the empirical fact that attacker in male, which is with great movement speed, is more frequently pass through the opponent by dribbling than that in female. In other words, the reason for higher success rate in dribbling in male sports is not necessarily that an attacker in male have high dribbling skills or a defender is not good at. It would be helpful to know the fact that the one-on-one outcomes are largely depend on the relationship between the movement speed and the response delay. For example, it may be better for an attacker in female not to try the dribbling by oneself but to try other attacks such as combination by passing. Also, the relationship between the movement speed and response delay provide the implication to the instruction because changes in movement speed and response (visuo-motor) delay due to body growth are generally not equal. For example, a defender who uses the time-optimal strategy may be able to defend well in childhood, but the number of defense failures may increase with growth. This is thought to be largely due to the human characteristic that the movement speed increases significantly compared to the response time that does not change much, from the childhood. Therefore, the finding that the outcome greatly depends on the relationship between the movement speed and the response delay would be useful for athletes and coaches to consider the tactics and the instructions.

6.4.2 Movement without a ball

The findings of my studies suggest that, when given a certain condition such as parameters of the agents and spatiotemporal constraints, the strategies are constrained by these and the behavioral outcomes (or expected successful rate) is approximately determined. This provides the insight that, in a series of plays in which a player receives a ball from a teammate and tries to dribble an opponent in actual games, the outcome of that play (i.e., successful attack or defense) may be determined at the moment of the player received the ball. In other words, this suggests that it is more important how a player moves before receiving a pass from a teammate rather than how to behave after receiving a pass. A study on three-on-one ball possession task in football have shown that skilled players take a position considering the position of the other players (Yokoyama & Yamamoto, 2011), and this suggests that positioning oneself to an advantageous situation is one of the skills in sports. That is, in the actual games, it would be critical for the successful attack to find a wide space and get a pass there. Conversely, the defender should not give the opponent a large space (i.e., give severe spatiotemporal constraints) by cooperating with teammates. The importance of movements without a ball has long been empirically emphasized in many sports. The results of my studies that agent behaviors and the outcomes are constrained by their environment may shed light on the importance of the movements without a ball.

6.5 Concluding remarks

The purpose of the present thesis was to explore the fundamental rules in human chase-and-escape behaviors from the macroscopic perspectives. Through the four studies, many aspects of human chase and escape strategies were found in common with other animals. These findings should provide the important insights into the chase-and-escape behavior, the sensorimotor control, and the evolution and learning, in animal species. Recently, it has been shown that the internal models established by human reaching movements also exist in insects by investigating chase behaviors in dragonflies (Mischiati et al., 2014). Perhaps, it might imply that the chase behavior is just a reaching movement to a fleeing target. Over the past several decades, there has been considerable progress in our understandings of the sensorimotor control and decision-making by numerous studies on reaching movements. However, it remains largely unknown how agents coordinate and improve the sensorimotor control and decision-making in order to accomplish own purpose in particularly continuous or evolutionary processes (Gallivan, Chapman, Wolpert, & Flanagan, 2018). I believe the chase-and-escape behavior observed in a wide range of species is an excellent subject to unveil these problems, and hope this thesis contributes to reveal these problems.

Supplementary information

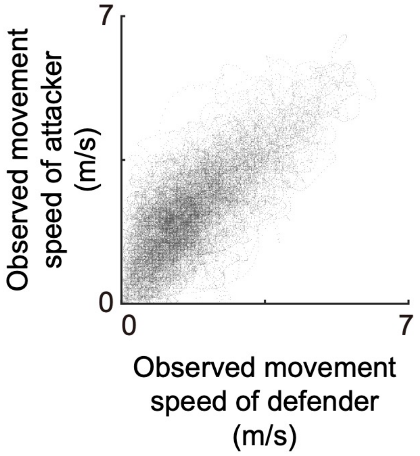

Figure S2-1 Observed movement speeds in real space

The scatter plot of the observed movement speeds between the attacker and defender in all trials in real space. Considering the visuo-motor delay, I set the speed of the defender at time i on the X axis and the speed of the attacker at time $i - \tau$ on the Y axis, where τ = 250 ms.

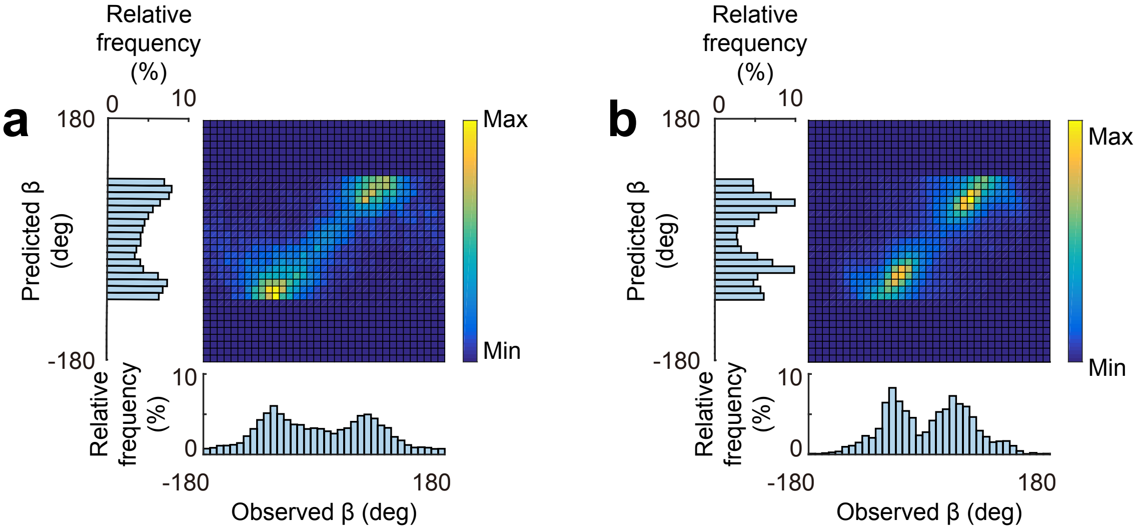

Figure S2-2 Histograms of the chase angles

(a) Histograms of the chase angles between observation and time-optimal model prediction of all data in real space (60 trials). The width of each bin and cell was set to 10 degrees. The bottom histogram shows the relative frequency of the observed chase angles. The left histogram shows the relative frequency of the predicted chase angles by the time-optimal model. The center 2D histogram shows the relative frequency between the observed and the predicted chase angles by the time-optimal model. This 2D histogram is same as the Figure 4a. (b) Histograms of the chase angles between observation and time-optimal model prediction of all data in virtual space (600 trials). The bottom and left histograms show the relative frequency of the observed and of the predicted chase angles, respectively. The center 2D histogram shows the relative frequency between the observed and the predicted chase angles, and is same as the Figure 4b.

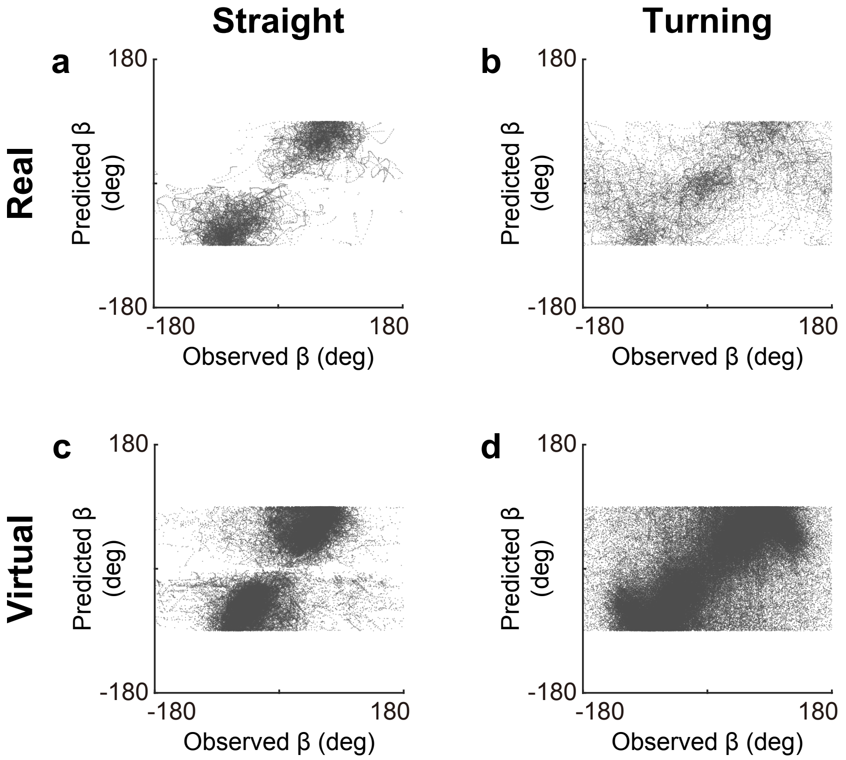

Figure S2-3 Scatter plot of chase angles

(a, b) The scatter plot between observed and predicted chase angles by the time-optimal model in real space (a) in straight and (b) in turning phases. (c, d) The scatter plot between observed and predicted chase angles by the time-optimal model in virtual space (c) in straight and (d) in turning phases.

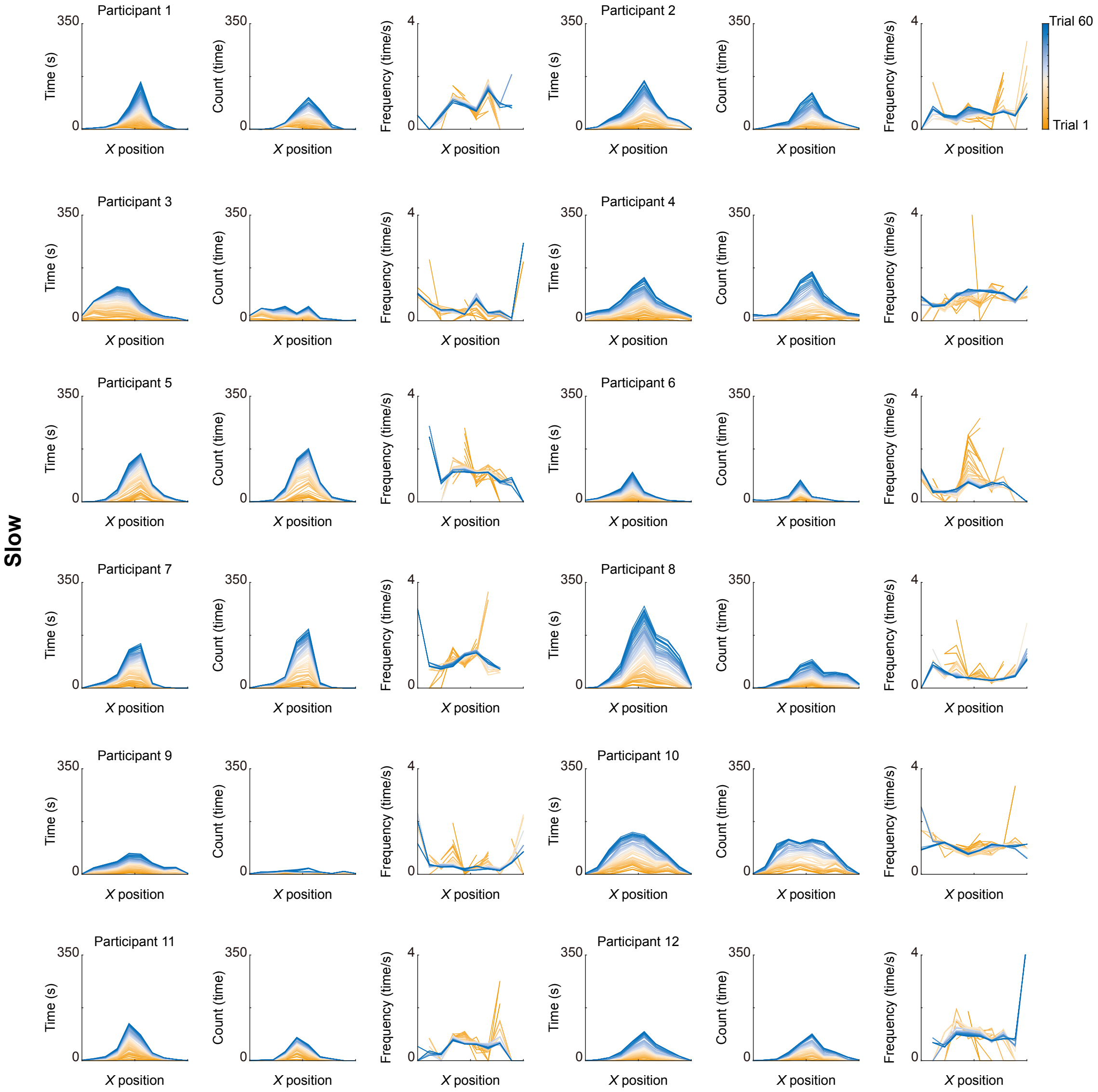

Figure S3-1 Cumulative changes in frequency regarding the direction changes of the attacker in each participant in slow condition.

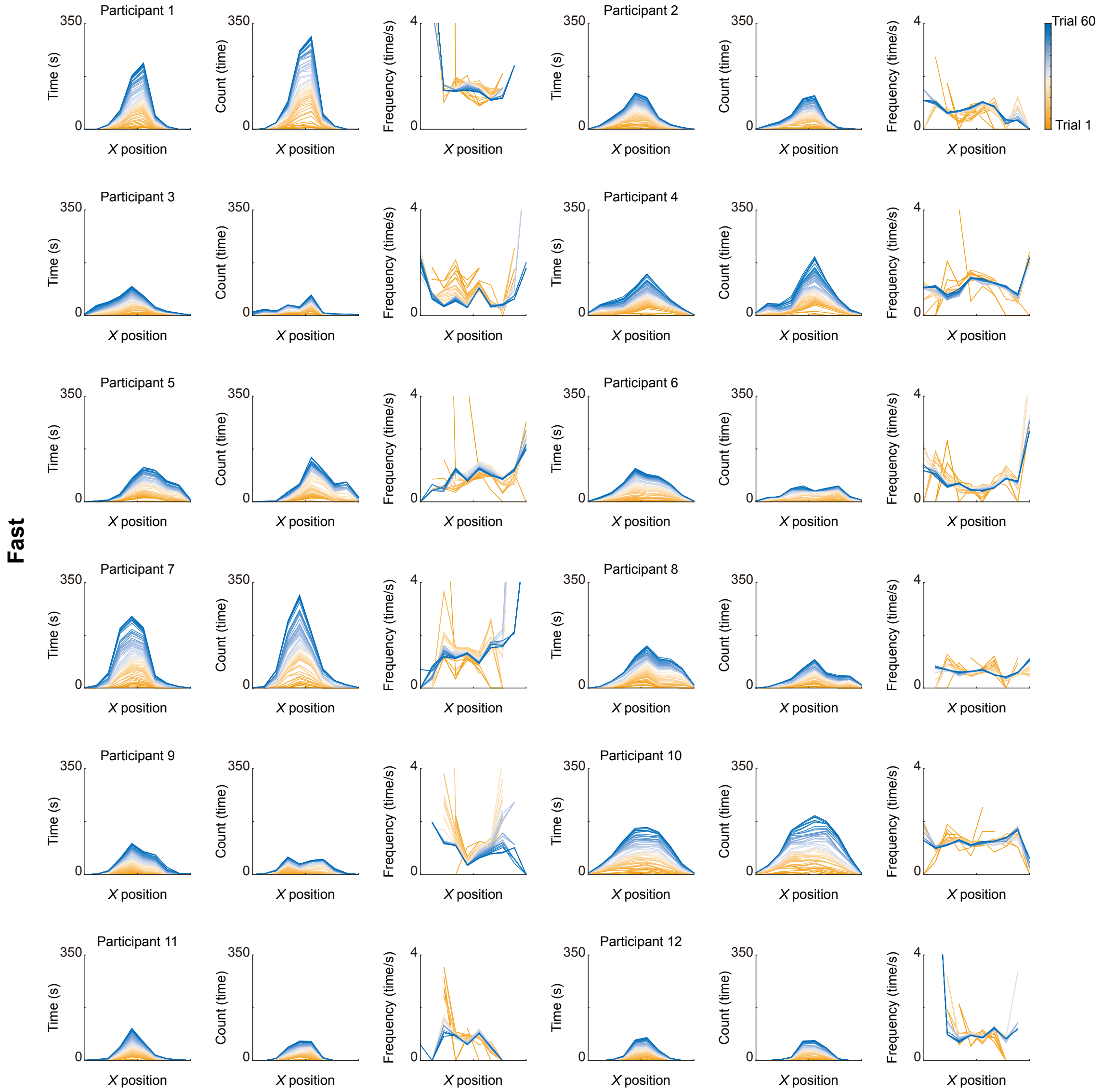

Figure S3-2 Cumulative changes in frequency regarding the direction changes of the attacker in each participant in fast condition.

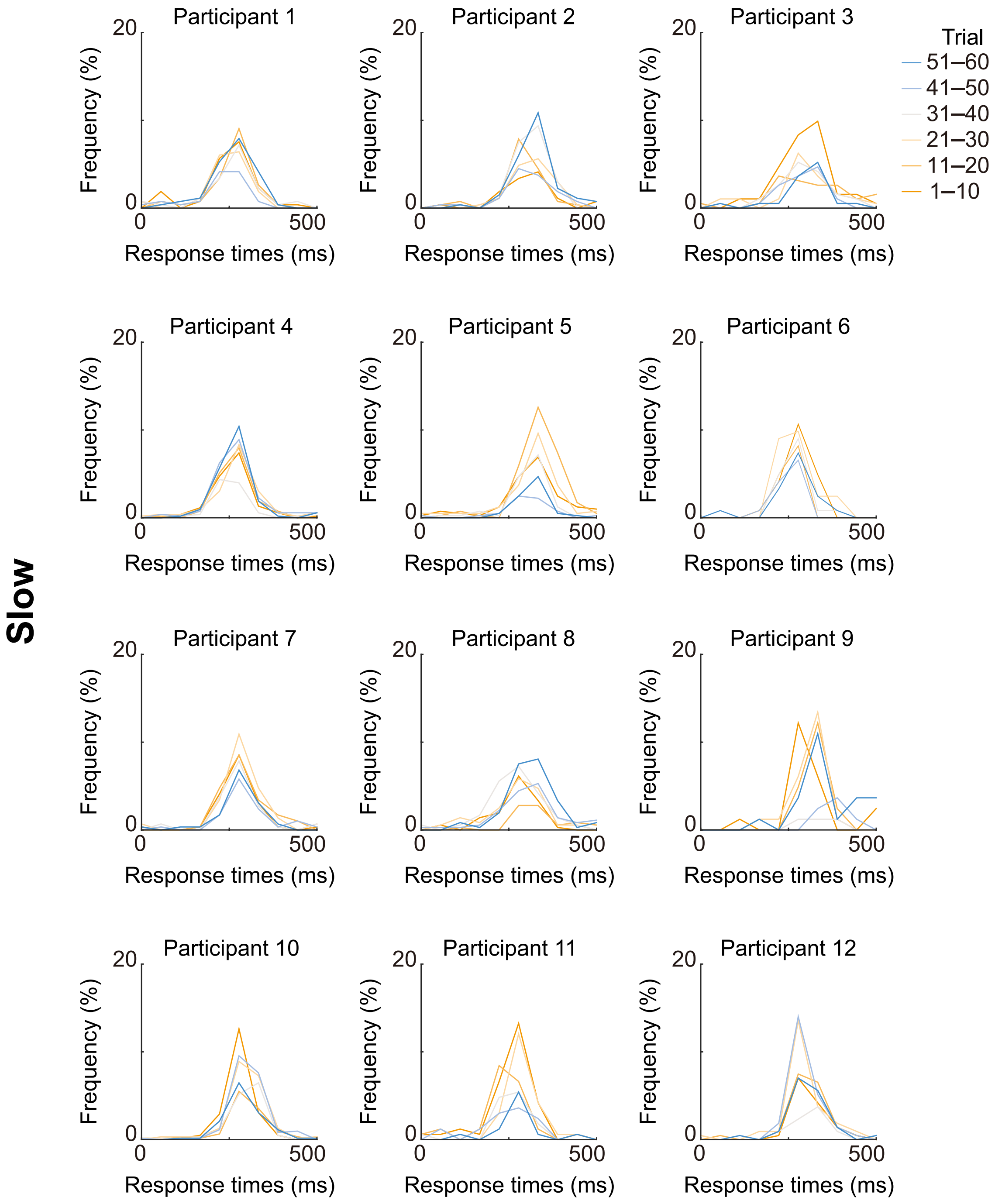

Figure S3-3 Histogram of the response time over time in each participant in slow condition. Each color represents a total of 10 trials.

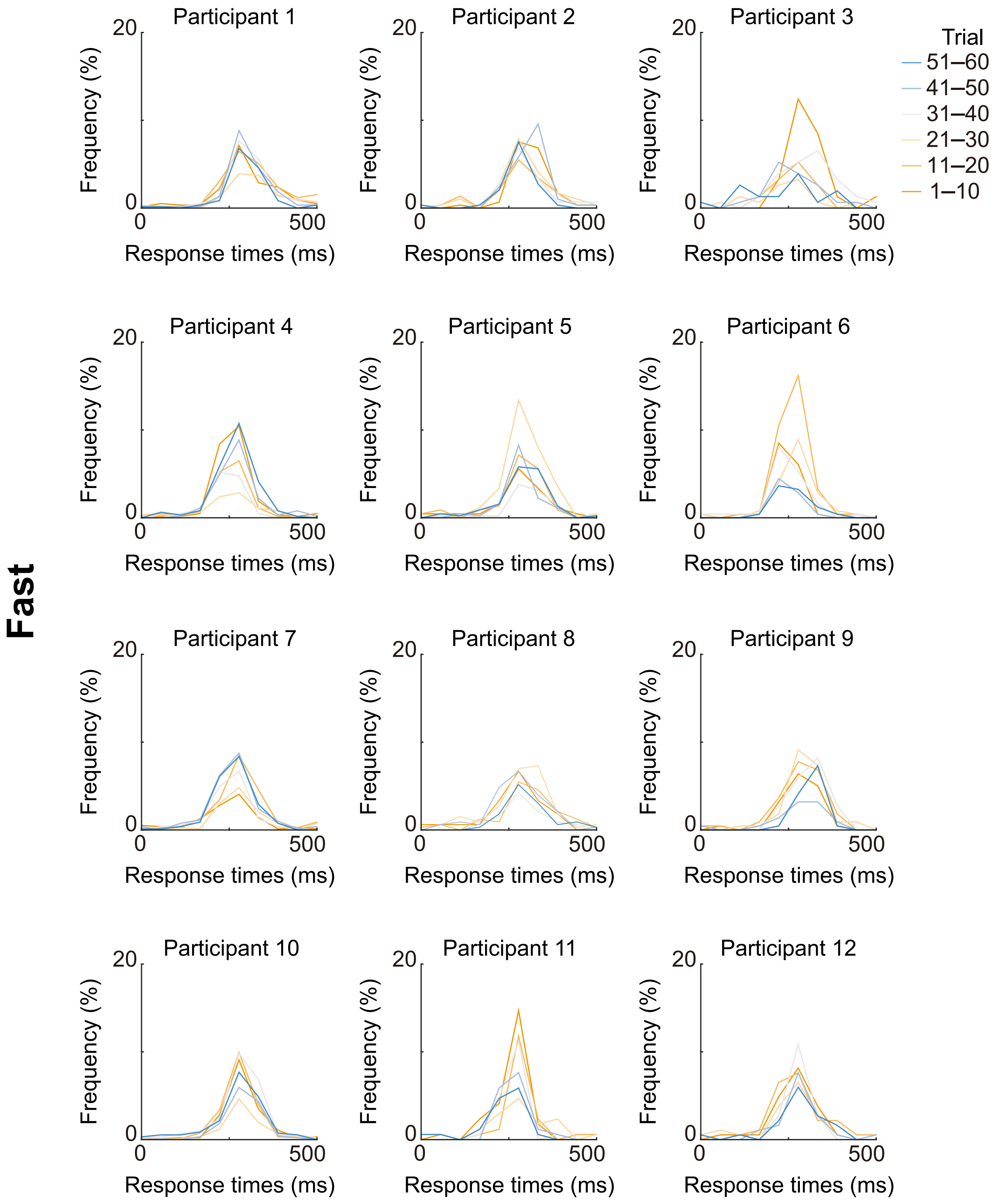

Figure S3-4 Histogram of the response time over time in each participant in fast condition.

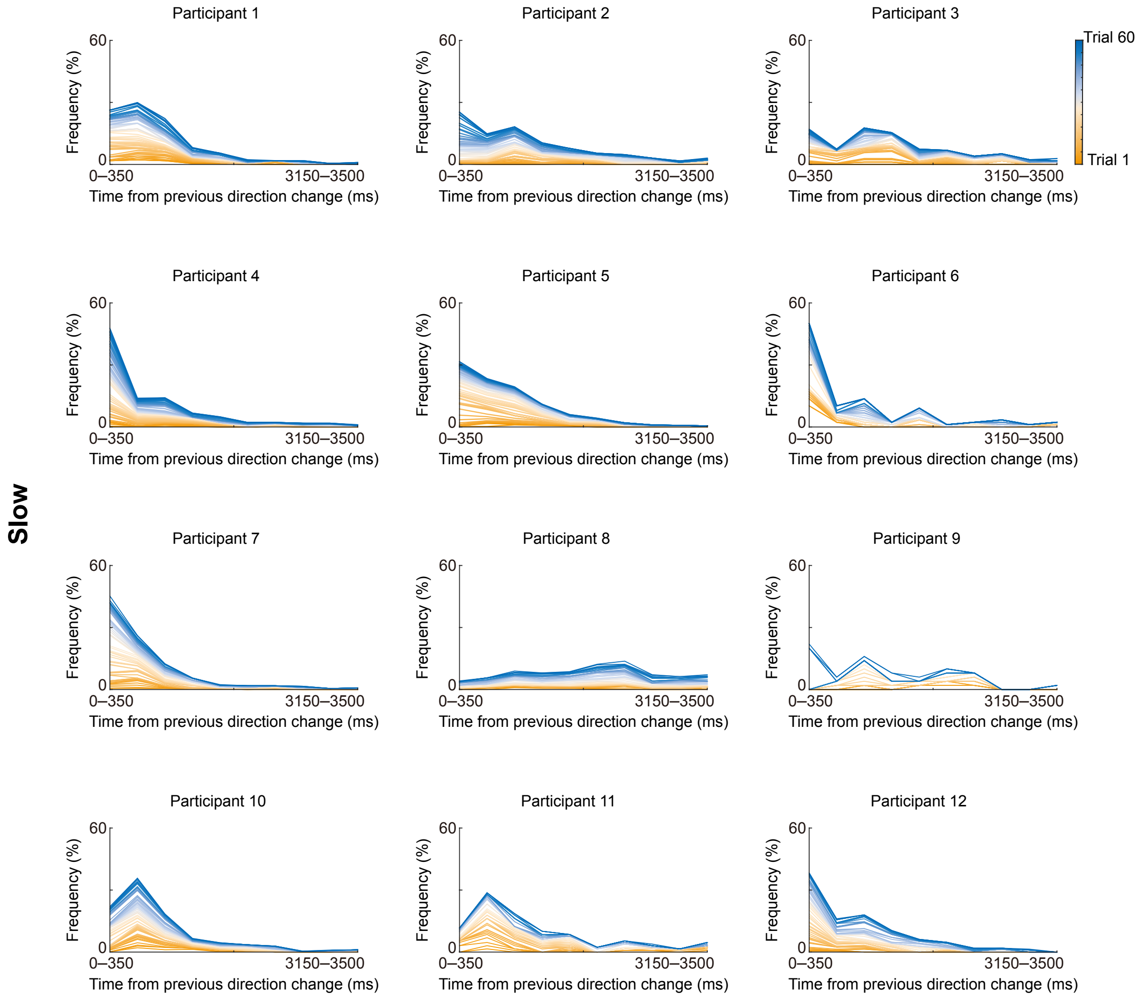

Figure S3-5 Cumulative changes of the time delay from the previous direction change in each participant in slow condition.

The time range was set from 0 to 3500 ms, and the range was divided into 10 separate time bins.

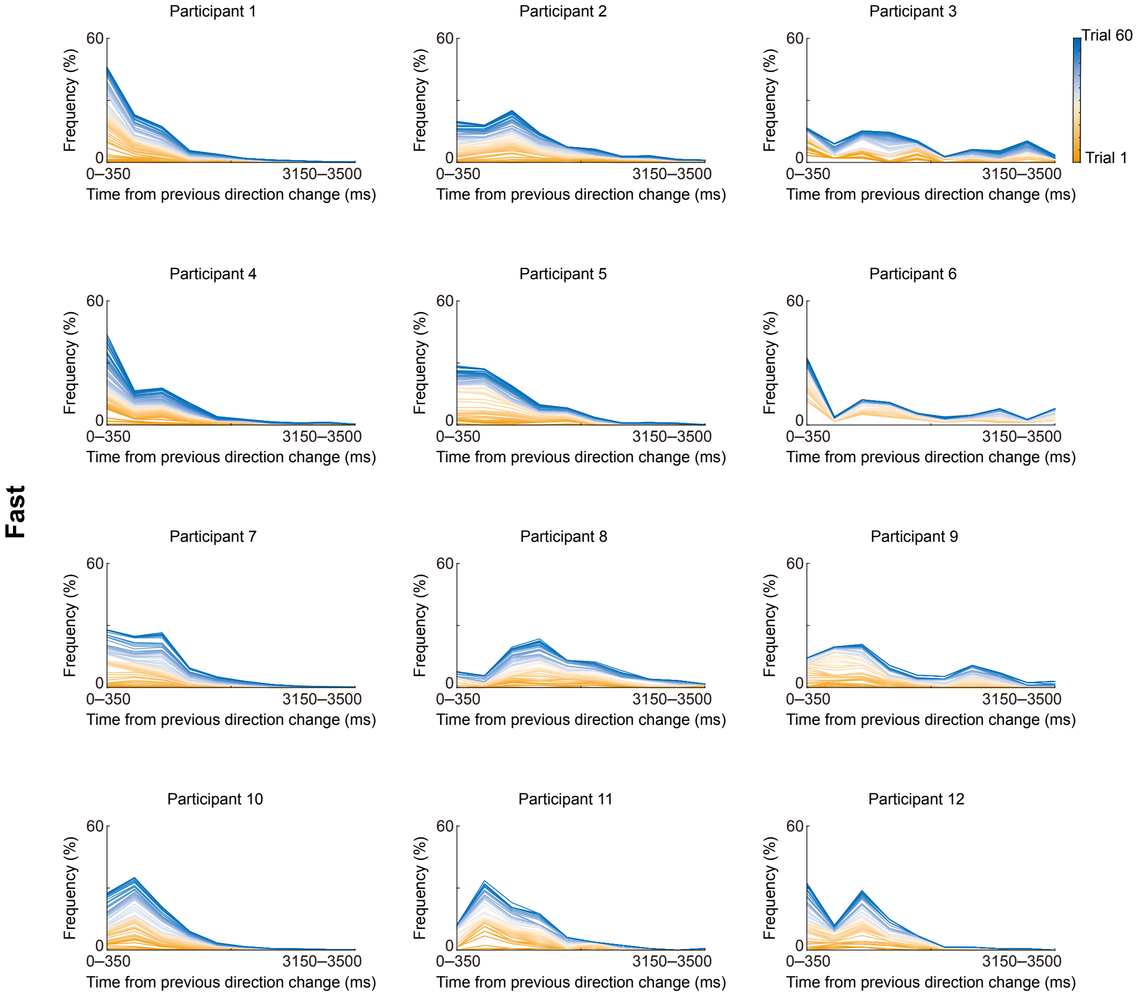

Figure S3-6 Cumulative changes of the time delay from the previous direction change in each participant in fast condition.

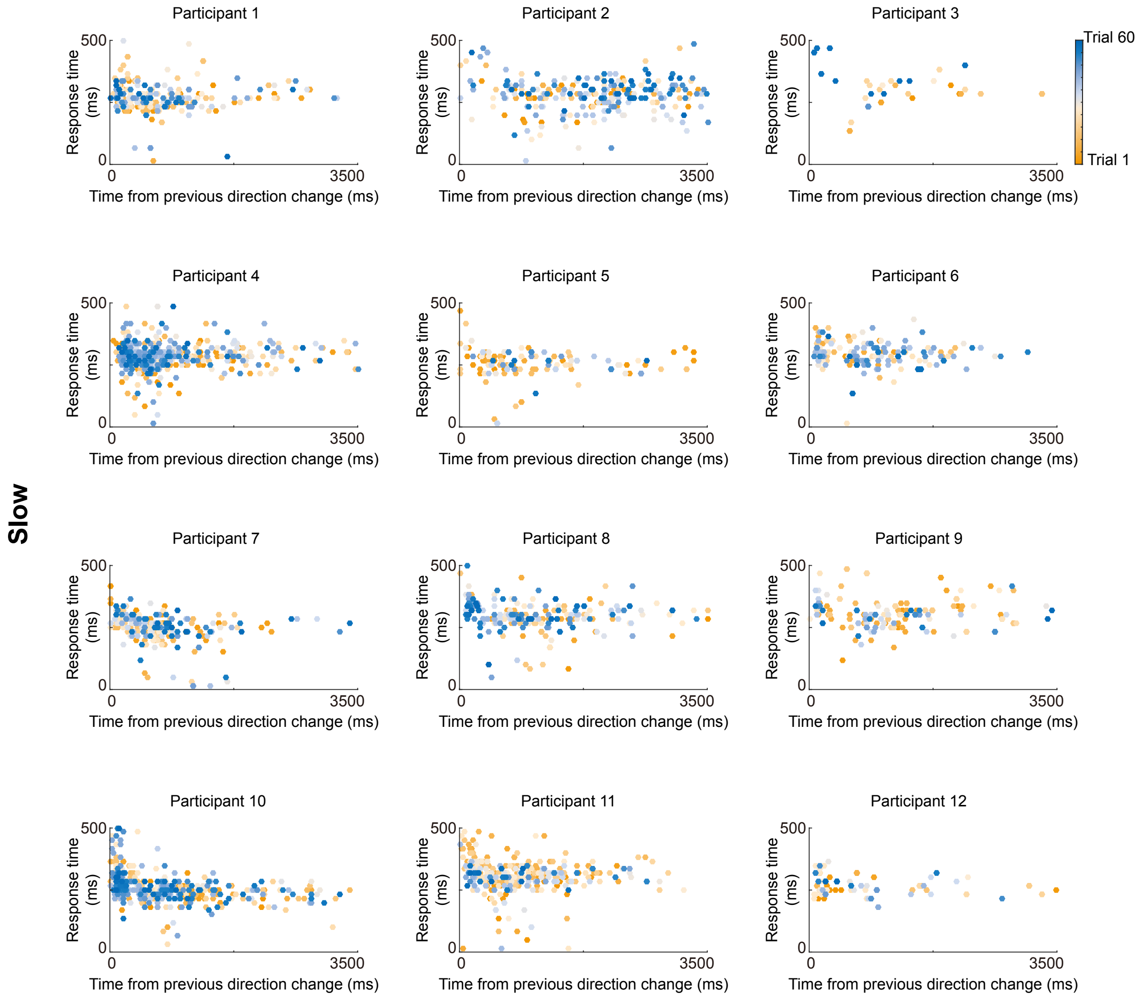

Figure S3-7 The response time to direction change with each time interval in each participant in slow condition.

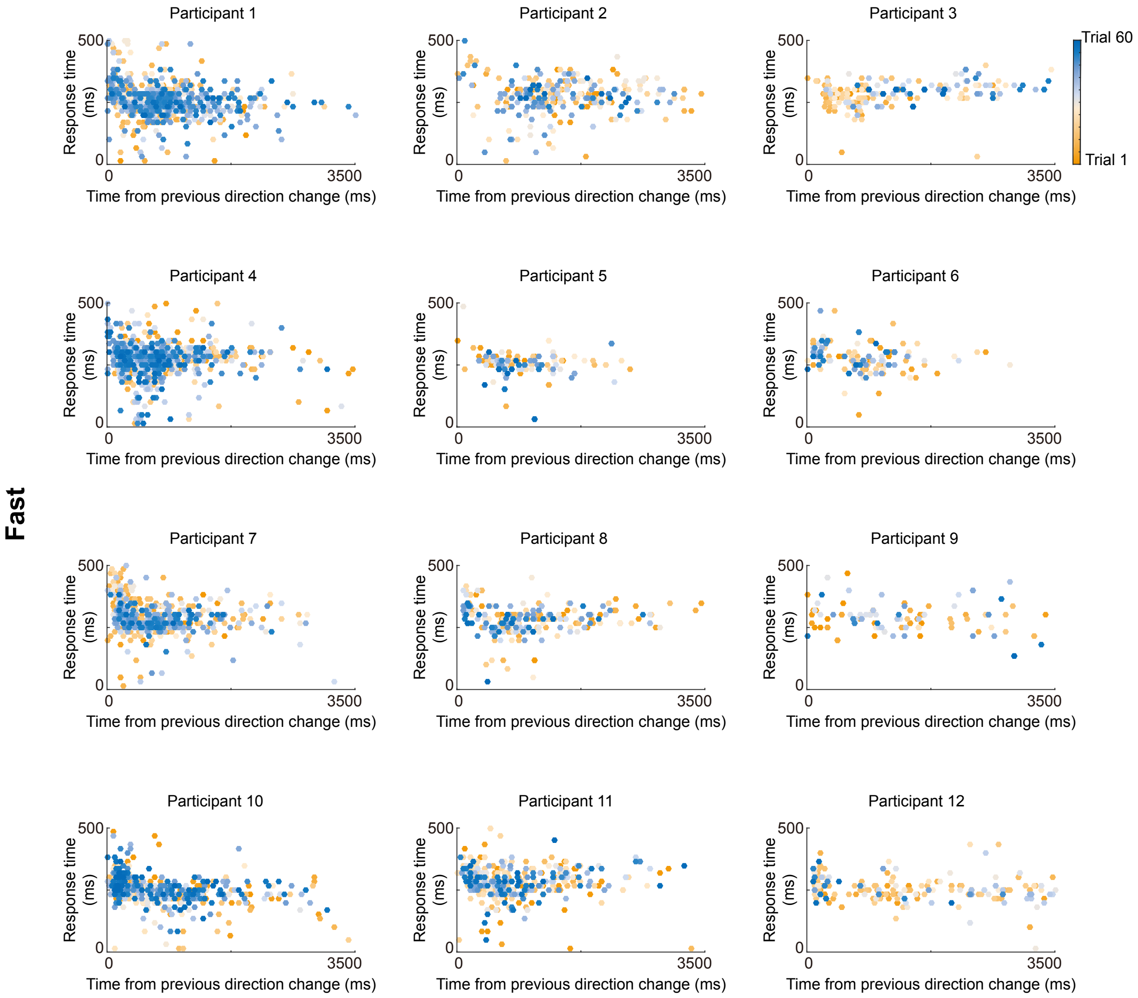

Figure S3-8 The response time to direction change with each time interval in each participant in fast condition.

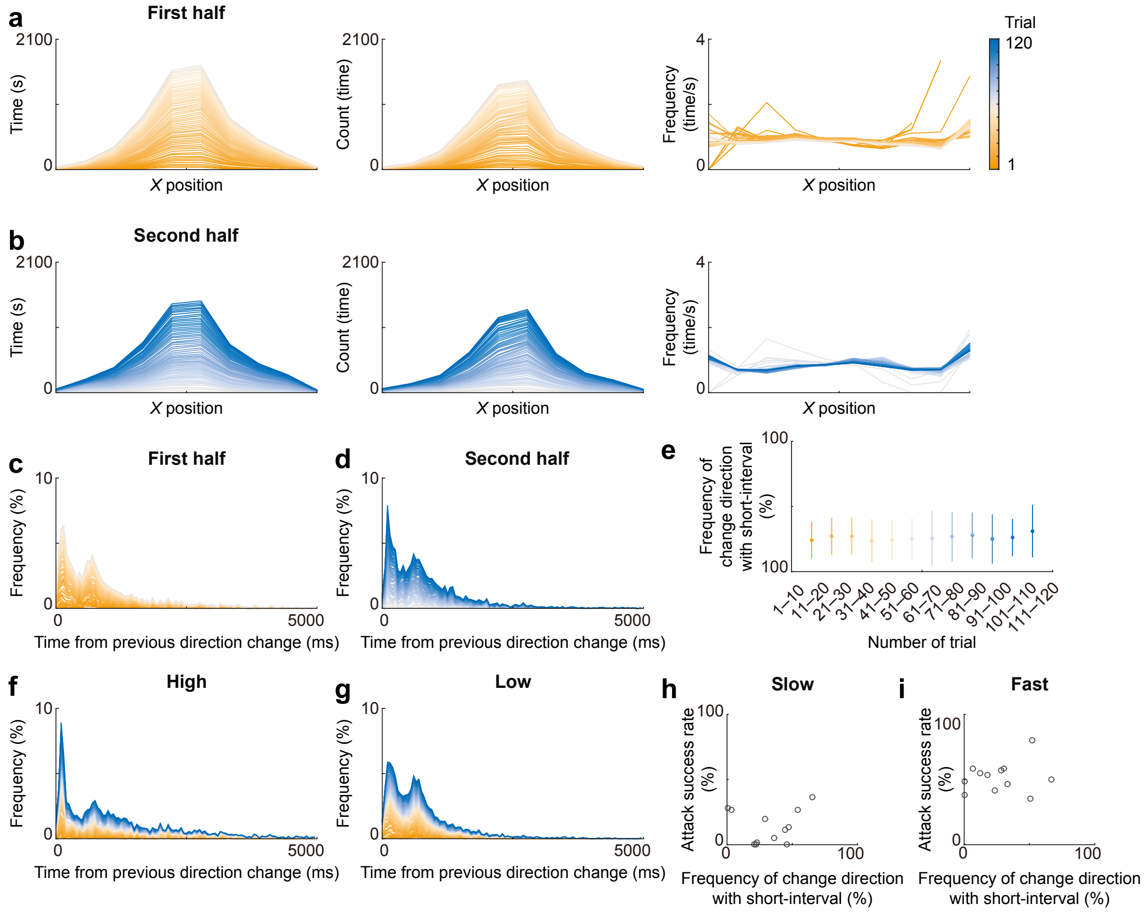

Figure S3-9 Cumulative changes of distributions relevant to attacker's direction change

(a-d) The group data of cumulative changes in frequency regarding the direction changes in "First half (1 to 60 trials)" and "Second half (61 to 120 trials)" in each participant. (e) The group data of the frequency of direction change with short-interval in each 10 trials over time. There was no significant difference between time bins of ten trials ($F_{11,\ 143} = 0.22$, $p = 0.99$, $\eta^2 = 0.018$). (f, g) The group data of cumulative changes of the time delay from the previous direction change in "High" and "Low" groups (each 6 participants) in successful attack rates using a median. (h, i) Correlations between the frequency of direction change with short-interval and successful attack rate. There were no statistically significant correlations ($r = 0.12$, $p = 0.72$ in slow condition; $r = 0.20$, $p = 0.54$ in fast condition; Figures c and d).

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