Title:

Action selection based on multiple-stimulus aspects in the wind-elicited escape behavior of crickets

Running title:

Behavioral choices of escaping crickets

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Summary statement:

When air currents triggering escape are faster and longer, crickets more frequently jump than run. Running speed and distance depend on stimulus velocity and duration, but direction control is independent.

25 **ABSTRACT**

26 Animals detect approaching predators via sensory inputs through various modalities and
 27 immediately show an appropriate behavioral response to survive. Escape behavior is
 28 essential to avoid the predator's attack and is more frequently observed than other
 29 defensive behaviors. In some species, multiple escape responses are exhibited with
 30 different movements. It has been reported that the approaching speed of a predator is
 31 important in choosing which escape action to take among the multiple responses.
 32 However, it is unknown whether other aspects of sensory stimuli, that indicate the
 33 predator's approach, affect the selection of escape responses. We focused on two
 34 distinct escape responses (running and jumping) to a stimulus (short airflow) in crickets
 35 and examined the effects of multiple stimulus aspects (including the angle, velocity, and
 36 duration) on the choice between these escape responses. We found that the faster and
 37 longer the airflow, the more frequently the crickets jumped, meaning that they could
 38 choose their escape response depending on both velocity and duration of the stimulus.
 39 This result suggests that the neural basis for choosing escape responses includes the
 40 integration process of multiple stimulus parameters. It was also found that the moving
 41 speed and distance changed depending on the stimulus velocity and duration during
 42 running but not during jumping, suggesting higher adaptability of the running escape. In
 43 contrast, the movement direction was accurately controlled regardless of the stimulus
 44 parameters in both responses. The escape direction depended only on stimulus
 45 orientation, but not on velocity and duration.

46

47 INTRODUCTION

48 Selecting a behavioral response appropriate to a situation is crucial for animals to
 49 survive events such as predator attacks. Vertebrates and invertebrates universally
 50 exhibit escape behavior to survive these attacks (Domenici et al., 2011a, b; LeDoux and
 51 Daw, 2018). Usually, animals quickly move away from the predator as a typical escape
 52 response, which increases their survival rate. The more emergent the situation is, the
 53 more predominantly the escape response is chosen compared to other defensive
 54 behaviors such as freezing (Baba and Shimozawa, 1997; Fadok et al., 2017; Evans et al.,
 55 2018; Turner et al., 2016). For instance, mice exhibit either a flight or freeze in response
 56 to the movement of the predator (De Franceschi et al., 2016); they choose the flight
 57 response when raptors approach them but exhibit freezing against raptors that just cruise
 58 past. This is because when the predator is unaware of the prey, freezing is more efficient
 59 to avoid being targeted. In contrast, once the predator is aware of the prey and begins to
 60 approach it, flight is an appropriate response to escape from the attack (Eilam, 2005).
 61 Since the animals of prey are subjected to attacks from various species of predators
 62 (Bulbert et al., 2015; Evans et al., 2019) and the approach of the predator varies trial by
 63 trial (Dangles et al., 2006; Walker et al., 2005), it is critical for the animals of prey to
 64 know how the predator approaches them, because it helps them make the appropriate
 65 behavioral choices against the emergency attack.

66 Animals detect the predator's approach through various parameters of sensory
 67 stimuli, such as speed, duration, and orientation (Domenici, 2010). For instance,
 68 stimuli with a higher velocity indicate a larger predator and quicker attack, and those
 69 with longer duration suggest greater movement of the predator (Casas and Dangles,
 70 2010). The orientation of the stimulus also indicates the direction from which the

71 predator approaches. Based on these characteristics of the stimuli, the prey regulates its
 72 escape response. The stimulus velocity and orientation are related to the escape distance
 73 and direction, respectively (Bhattacharyya et al., 2017; Card, 2012; Domenici et al.,
 74 2011a, b; Dunn et al., 2016; Stewart et al., 2013). The size of the looming stimulus
 75 indicates the distance of the approaching predator and has been known to determine
 76 escape initiation in several species (Bhattacharyya et al., 2017; Dunn et al., 2016;
 77 Fotowat and Gabbiani, 2007; Preuss et al., 2006). The escape behavior of various
 78 animals employ multiple types of responses with distinct movements (Briggman et al.,
 79 2005; Liu and Hale, 2017; Takagi et al., 2017), resulting in different locomotor
 80 performance. Each escape response is considered to have a different advantage in
 81 performance, such as speed or controllability, which affect the success rate of avoidance
 82 from the predator's attack (Card and Dickinson, 2008; Sato et al., 2019). Recent studies
 83 suggest that the approaching speed of the predator indicated by the stimulus velocity has
 84 an impact on the action selection between different escape responses, such as short and
 85 long modes of flies taking-off (Card and Dickinson, 2008; von Reyn et al., 2014, 2017).
 86 However, it is unknown what other parameters, including the direction or duration of
 87 the stimulus, are involved in the action selection for escaping.

88 We addressed this issue using the wind-elicited escape behavior of the field
 89 cricket *Gryllus bimaculatus* as the experimental material. Crickets exhibit either running
 90 or jumping in response to a short air current that is detected as a predator's approach
 91 (Dupuy et al., 2011; Sato et al., 2017, 2019). The running and jumping movements are
 92 different from each other: the crickets either run on the ground or jump by strongly
 93 kicking the ground. Our previous study has revealed a "trade-off" between speed and
 94 behavioral flexibility: if crickets choose to run rather than jump, they move more slowly

95 but can respond more flexibly to further attacks received during the response (Sato, et
96 al., 2019). Interestingly, crickets can also control their movement direction accurately in
97 response to the stimulus from any direction, not only during running but also while
98 jumping (Sato et al., 2019), in contrast to escape by jumping in locusts (Santer et al.,
99 2005; Simmons et al., 2010). Besides, the longer the stimulus, the longer the distance
100 the crickets run (Oe and Ogawa, 2013). These facts suggest that crickets may be able to
101 take multiple stimulus parameters into account while choosing either to run or jump.

102 In this study, we manipulated the three parameters of an air-current stimulus,
103 (angle, velocity, and duration) and examined their effects on the response probabilities
104 to run and jump those were elicited by the stimulus. Furthermore, to clarify the impacts
105 of these parameters on the performance in the escape responses, we examined the
106 relationships between the locomotor parameters, which included movement speed,
107 travel distance, reaction time, directionality, and other stimulus parameters. Our results
108 demonstrate that crickets choose the escape response and regulate their locomotion
109 based on multiple stimulus parameters.

110

111 MATERIALS AND METHODS

112 Animals

113 We used the wild-type strain of crickets (*Gryllus bimaculatus*, Hokudai WT; Watanabe
114 et al., 2018) that were bred in our laboratory. Thirty adult male crickets, less than 14
115 days after adult molting, were used throughout the experiments. They were reared under
116 12/12 h light/dark conditions at a constant temperature of 27°C. All experiments were
117 conducted during the dark phase at 26-28°C.

118

119 Behavioral experiment

120 The experimental apparatus as per our previous study (Sato et al., 2019) was used
121 throughout the experiments. We monitored the wind-elicited escape responses using a
122 high-speed digital camera (CH130EX, Shodensha, Osaka, Japan) installed above a
123 circular arena ($\phi = 260$ mm). After anesthetization by cooling with ice (0 °C) for 10 min,
124 crickets were marked with two white spots on the dorsal surface of the head and thorax,
125 the size of which was large enough to detect the movement of crickets from images. All
126 experiments were performed after 30 min to make sure they completely recover from
127 anesthetization. The cricket was placed in the center of the arena inside an inverted
128 beaker ($\phi = 50$ mm) covered with aluminum foil. After the beaker was carefully lifted,
129 an air-current stimulus was immediately applied to the cricket that was standing still,
130 and the response was recorded by the camera. Based on the video data (shutter speed, 1
131 ms; sampling rate, 120 frames s⁻¹; total recording duration, 1660 ms), the two markers
132 on the animal were automatically traced, and locomotor parameters mentioned in a later
133 section were measured using motion analysis software (Move-tr/2D, Library, Tokyo,
134 Japan). To monitor the entire trajectory during movement, we adopted a 285.7×285.7

135 mm frame size with 1024×1024 pixels resolution, which covered the entire arena.

136

137 **Stimulation and experimental procedure**

138 The air-current stimulus used throughout the experiments was a short puff of nitrogen
139 gas from a plastic nozzle ($\phi = 15$ mm) connected to a pneumatic picopump (PV820,
140 World Precision Instruments, Sarasota, FL, USA). One air-current nozzle was installed
141 on the inside wall of the arena to be positioned on the same horizontal plane as the
142 animal. Since the crickets were oriented randomly within a beaker, the stimulus angles
143 measured as the angles of the crickets' orientation against the stimulus source (left in
144 Fig. 1A) were varied across the trials.

145 The data of three experiments with different stimulation were analyzed to test
146 the effect of the three stimulus parameters on escape responses: "angle test," "velocity
147 test" and "duration test." A part of the data obtained in our previous study (Sato et al.,
148 2019) was also analyzed for the angle test, in which the effect of stimulus angles was
149 examined in the escape responses to a constant stimulus duration of 200 ms and velocity
150 of 834 mm s^{-1} . The travel time of the air current to the center of the arena was
151 14.6 ± 0.1 ms, which was calculated based on the delay in stimulus-evoked ascending
152 spikes of projection neurons that were extracellularly recorded ($N = 2$ animals, 10 trials
153 in total). In the velocity test, we examined the effect of stimulus velocities on the escape
154 response to the stimuli of 200 ms duration with four different velocities (340, 618, 734,
155 and 834 mm s^{-1}) (left in Fig. 1C). The travel times of these stimuli were 21.2 ± 1.0 ,
156 15.5 ± 0.1 , 14.6 ± 0.1 and 14.6 ± 0.1 ms for 340, 618, 734 and 834 mm s^{-1} of air
157 currents, respectively ($N=2$ animals, 10 trials in total for each stimulus velocity). In the
158 duration test, we examined the effect of stimulus duration on the escape response to the

159 stimuli of 834 mm s^{-1} for four different durations (20, 40, 60, 80, and 100 ms) (left in
160 Fig. 1E). The velocity and duration of the air current were regulated by air pressure and
161 using the interval between the opening and closing of the valve of the picopump.

162 In the angle test, 20 trials were repeatedly performed for each individual at
163 inter-trial intervals of 60–90 s. In both the velocity and duration tests, stimuli with
164 different velocities or durations were applied to the same individuals at increasing ($N=5$
165 animals) or decreasing order ($N=5$ animals). Twenty trials were performed in one
166 session for each type of stimulus, so in total, 80 or 100 trials were performed for each
167 individual in tests. The crickets were rested between the sessions for approximately 10
168 min within a plastic container ($138 \text{ mm} \times 220 \text{ mm} \times 135 \text{ mm}$) and freely accessed food
169 and water. Ten crickets were tested for each experiment.

170

171 **Data analysis**

172 The wind-elicited responses were analyzed as in our previous study (Sato et al., 2017,
173 2019). Responses were defined based on the translational velocity of the cricket
174 movement. If the velocity exceeded 10 mm s^{-1} within 250 ms after the stimulus onset
175 and was greater in its maximum value by more than 50 mm s^{-1} , the cricket was
176 considered to respond to the stimulus. If the cricket did not begin to move within 250
177 ms of the response definition period, the trial was considered as “no response.” For the
178 angle test, the data in all trials were pooled, and then the response probability was
179 calculated from the number of responding trials per total trials for the range of every 20
180 degree of stimulus angles (right in Fig. 1A). In the velocity and duration tests, the
181 response probability was calculated from the number of responding trials per 20 trials
182 for each type of stimulus (right in Fig. 1C,E).

183 As in our previous study (Sato et al., 2019), the wind-elicited responses were
 184 categorized into “running” or “jumping” according to the movement of legs during the
 185 locomotion, which was confirmed visually for all responding trials by frame check of
 186 the video. If all six legs were off the ground simultaneously, the response was defined as
 187 “jumping,” if any one of the six legs touched the ground during movement, that
 188 response was defined as “running” (Fig. S1A). We rarely observed complex behaviors
 189 combined with running and jumping, such as jumping after running and *vice versa*. The
 190 selection ratio of running or jumping was calculated as the proportion of responses for
 191 all responding trials. In the angle test, all trials were pooled and divided into four groups
 192 based on the range of absolute stimulus angle, 0–45, 45–90, 90–135, and 135–180, and
 193 the selection ratio was calculated for each angular range (Fig. 1B). In the velocity and
 194 duration tests, the selection ratio was calculated for each type of stimulus, regardless of
 195 the stimulus angle (Fig. 1D,F).

196 We focused on the “initial response” in the responding trial and analyzed the
 197 cricket’s movement during the initial response as defined in our previous studies
 198 (Fukutomi et al., 2015; Oe and Ogawa, 2013; Sato et al., 2017, 2019). The initial
 199 response was the first continuous movement (bout) in which the translational velocity
 200 was greater in its maximum value than 50 mm s^{-1} and never less than 10 mm s^{-1} after
 201 the stimulus onset. Therefore, the response start was measured as the time when the
 202 translational velocity exceeded 10 mm s^{-1} after stimulus onset and the response finish
 203 was measured as the time when the velocity was less than 10 mm s^{-1} . Movement
 204 distance, maximum translational velocity, and reaction time were measured as the
 205 metric locomotor parameters that characterized the response movements. The
 206 movement distance was measured as the entire path length of the moving trajectory. The

207 reaction time was calculated by subtracting the mean travel time of the air current, as
 208 mentioned above, from the time from the opening of the picopump to the start of the
 209 response. Angular parameters including movement direction and turn angle were
 210 calculated based on the cricket's body axis, as a vector connecting the thoracic and head
 211 markers (Fig. S1B). The movement direction was measured as the angle between the
 212 body axis at the starting point of the response and a line connecting the thoracic markers
 213 at the start and finish points. Thus, if the cricket moved in the direction opposite to the
 214 stimulus source, the movement direction would be equal to the stimulus angle. Since it
 215 has been confirmed in a previous study that crickets move in the opposite direction to
 216 the stimulus in both running and jumping (Sato et al., 2019), the accuracy in the
 217 directional control was assessed by the absolute value of the difference between the
 218 movement direction and stimulus angle. The turn angle was measured as the angle
 219 between the body axes at the start and finish points. If the cricket is oriented to the exact
 220 opposite side of the stimulus source at the finish points, the turn angle would be equal to
 221 the stimulus angle.

222

223 **Statistical analysis**

224 R programming software (ver. 3.4.4, R Development Core Team) was used for all the
 225 statistical analyses. We assessed the effect of the stimulus parameters on the response
 226 probability and selection ratio, both of which were calculated for each individual, using
 227 multiple logistic regression analysis in each of the angle, velocity, and duration tests. In
 228 addition to the manipulated stimulus parameter, the trial order was considered as an
 229 explanatory variable, as follows:

230

$$(Response\ probability) = \frac{1}{1 + \exp(-(a(Stimulus\ parameter) + b(Trial\ order) + c))}, \quad (1)$$

232

$$(Selection\ ratio) = \frac{1}{1 + \exp(-(a(Stimulus\ parameter) + b(Trial\ order) + c))}, \quad (2)$$

234

235 where a and b are the estimated coefficients, and c is the intercept. Then, the
236 significance of the coefficients for stimulus parameters as explanatory variables was
237 checked to assess their effect on the response probability or selection ratio (Table 1).

238 To analyze the relationships between the metric locomotor parameters, such as
239 movement distance, maximum velocity, or reaction time, and the stimulus angle, which
240 was indicated as an absolute value in degrees from 0 (front) to 90 (lateral) and 180
241 (behind), we used linear regression analysis as follows:

242

$$(Metric\ locomotor\ parameter) = a(Stimulus\ angle) + b, \quad (3)$$

244

245 where a is the estimated coefficient and b is the intercept. The significance of the
246 coefficients was checked to assess the effect of the stimulus angle on the metric
247 parameters (Table 2).

248 Since the response probability and selection ratio were strongly affected by
249 stimulus velocity and duration, the sample size of data for the locomotor parameters
250 varied among the sessions using different types of stimuli. In particular, slow (340 mm
251 s⁻¹ of velocity) or short (20 ms of duration) air current rarely or never elicited jumping;
252 therefore, we could not calculate the mean value of the locomotor parameters for each
253 tested individual in the session using such stimuli. Considering the small and varied

sample sizes, a linear mixed-effects model (LMM, the package ‘lme4’ ver. 1.1-23 in R) was adopted to assess the effects of stimulus velocity and duration on the locomotor parameters. We assumed the LMMs with stimulus parameters as explanatory variables, as follows:

$$(Locomotor\ parameter) = \beta_0 + \beta_1(Stimulus\ parameter) + r, (4)$$

where β_0 is the intercept, β_1 is the estimated coefficient, and r is the random effect that the animal IDs were considered. The significance of the effect of stimulus parameters was tested by comparing the LMMs with and without the explanatory variable of stimulus velocity or duration by the likelihood ratio test (Table 3).

Relationships between angular parameters and stimulus angle were analyzed by the regression analyses, which were used in our previous study (Sato et al., 2019). The movement direction was considered as non-circular data and linear regression analysis was used as follows:

$$(Movement\ direction) = a(Stimulus\ angle) + b, (5)$$

where a is the estimated coefficient and b is the intercept (Table 4). In contrast, the turn angle was considered as circular data, and circular regression analysis was used as follows:

$$(Turn\ angle) = \tan^{-1} \left(\frac{A+B\cos(Stimulus\ angle)+C\sin(Stimulus\ angle)}{a+b\cos(Stimulus\ angle)+c\sin(Stimulus\ angle)} \right), (6)$$

278 where A and a are the intercepts, B and b are the estimated coefficients of cosine,
279 and C and c are the estimated coefficients of sine in the numerator and denominator
280 of the model, respectively.
281

282 **RESULTS**

283 **Faster and longer stimulus elicited the jumping response more frequently**

284 First, we examined the parameters of the stimulus that affected the action selection of
 285 either running or jumping. We tested the effects of angle, velocity, and duration of the
 286 stimulus, and found that the crickets chose to jump more frequently in response to the
 287 faster and longer stimuli (Fig. 1; Table 1). In the angle test (Fig. 1A,B), the crickets
 288 likely chose jumping rather than running in response to the stimulus from behind
 289 (approximately 0 degree), but the effect of stimulus angle on the selection ratio of
 290 running or jumping was not statistically significant (Table 1). In contrast, the velocity
 291 and duration tests demonstrated that the velocity and duration of the stimulus apparently
 292 affected both probabilities of the escape response to the stimulus and the selection ratio
 293 of running and jumping while escaping (Fig. 1C–F). The response probability and the
 294 ratio of jumping choice to running choice significantly increased as the velocity or
 295 duration of the stimulus increased (Table 1). These results indicated that the cricket's
 296 choice of escape responses was affected by the two stimulus parameters, velocity and
 297 duration of the air current. Although we repeated multiple trials for each individual, the
 298 trial orders did not affect the response probabilities or selection ratios in all three
 299 experiments (Fig. 1; Table 1).

300

301 **Crickets changed running speed depending on stimulus parameters**

302 Based on the data from the angle, velocity, and duration tests, we investigated the
 303 effects of stimulus parameters on locomotion performance indicated by metric
 304 locomotor parameters. These included movement distance, maximum velocity, and
 305 reaction time, in running and jumping. The relationships between these parameters and

the stimulus angle indicated that the crickets changed their locomotion performance according to the stimulus angle during running rather than during jumping (Fig. 2). The stimulus angle had a significant impact on all three metric locomotor parameters during running but only on the maximum velocity during jumping (lines in Fig. 2; Table 2). The closer to behind of the cricket the stimulus was applied from, the quicker the crickets began to respond and the farther and faster they ran (left in Fig. 2A–C). In contrast, the closer to front of the cricket the stimulus angle, the faster the crickets jumped, but the movement distance and reaction time of jumping were not significantly affected by the stimulus angle (right in Fig. 2A–C).

In the velocity and duration tests, we examined the effects of velocity or duration of the stimulus not only on the metric locomotor parameters (Figs. 3 and 4) but also on the movement direction (Figs. 5 and 6) of running and jumping. The stimulus velocity and duration influenced the metric locomotor parameters of running rather than jumping. The velocity test indicated that the crickets increased the movement distance and speed during running, but not during jumping, as the stimulus velocity increased (Fig. 3A,B; Table 3). The reaction time became shorter as the stimulus velocity increased in both running and jumping, meaning that the faster the air current, the quicker the crickets initiated the escape regardless of the response type (Fig. 3C; Table 3). In the duration test, the longer the stimulus, the farther and faster the cricket ran, but they did not change their jumping locomotion with the stimulus duration (Fig. 4). The effects of the stimulus duration were significant on all of the metric locomotor parameters during running, whereas none of the parameters in jumping (Table 3). Interestingly, the longer the stimulus, the earlier the cricket started the escape running but did not change the start of jumping. This was probably because the shortest stimulus

330 (20 ms) elicited running responses with a long latency of over 100 ms after the stimulus
331 was terminated (left in Fig. 4C). If the stimulus is too short, it may take longer for the
332 crickets to notice it, or such a stimulus would be judged as not dangerous.

333

334 **Movement direction was controlled regardless of stimulus velocity and duration**

335 Our previous studies have shown that crickets precisely control their movement
336 direction against the stimulus angle during both running and jumping (Sato et al., 2019).
337 We then examined whether the velocity and duration of the stimulus affected the
338 directional control of the cricket escape responses (Figs. 5 and 6). The crickets could
339 control their movement direction precisely against the stimulus angle, independent of
340 the velocity and duration of the stimulus. Even in response to stimuli of different
341 velocities or durations, plots of the movement direction against stimulus angle were
342 distributed close to the $y = x$ line during running and jumping (Figs. 5A and 6A; Table
343 4). Here, how precisely the crickets moved in the opposite direction to the stimulus was
344 assessed by the absolute value of the angular difference between the moving direction
345 and stimulus angle. Independent of the stimulus velocity, the absolute angular
346 differences between the movement direction and stimulus angle were approximately 30
347 degree in both running and jumping (Fig. 5B; Table 3), indicating no effect of the air
348 current velocity on the directional control. Also, in the duration test, the duration of the
349 stimulus had little impact on the directional control of the escape responses (Fig. 6). The
350 absolute angular difference between the movement direction and stimulus angle was
351 mostly constant for the stimuli of 40–100 ms duration both in running and jumping (Fig.
352 6B). The significant effect of the stimulus duration was observed in running but not in
353 jumping (Table 3), which may be because the running directions in response to the

354 shortest (20 ms) stimulus were less correlated with the stimulus angle. In contrast, no
 355 jumping was elicited by the shortest stimuli, resulting in no significant difference in the
 356 absolute difference value of the stimulus duration in jumping. We also checked the
 357 impact of the velocity and duration of the stimulus on the relationship between the turn
 358 angle and stimulus angle (Figs. S2 and S3) but observed no apparent difference in the
 359 distributions of the plot among the responses either in the velocity test or in the duration
 360 test. Thus, the angular parameters of escape responses, including the movement
 361 direction and turn angle, were not significantly affected by the velocity and duration of
 362 the stimulus, except for extremely short stimuli that were close to the threshold to
 363 induce jump.

364 To conclude regarding the impacts of stimulus parameters on locomotor
 365 parameters, crickets altered their locomotion performance, such as the moving distance,
 366 velocity, and reaction time, according to the angle, velocity, and duration of the stimulus
 367 during running but hardly during jumping. In contrast, the escape direction was
 368 controlled precisely, independent of the velocity and duration of the stimulus in both
 369 running and jumping escape responses. These results suggest that movement
 370 performance in speed and distance is modulated during the running response but not
 371 while jumping, which depends on the stimulus characteristics. Directionality of the
 372 escape movements was dictated by the stimulus angle only, but was unaffected by the
 373 stimulus intensity and duration.

374

375 **DISCUSSION**

376 **The neural system to choose escape response is based on multiple stimulus** 377 **parameters**

378 The prey animal must perceive how the predator approaches through multiple aspects of
379 the stimulus in order to perform the most successful escape response. Previously, the
380 choice of escape response has been reported to depend on stimulus velocity
381 (Bhattacharyya et al., 2017; von Reyn et al., 2014, 2017). Our results revealed that both
382 velocity and duration of the stimulus affect the action selection of either running or
383 jumping in the wind-elicited escape behavior of crickets. In conclusion, crickets likely
384 made a decision regarding their escape responses based on multiple aspects of the
385 air-current stimuli that indicate the predator's approaches. This finding strongly
386 suggests that there is an integration process of multiple channels of distinct stimulus
387 information for action selection in the crickets' central nervous system.

388 While complex neural mechanisms across multiple brain regions are involved
389 in mammalian escape behaviors (Evans et al., 2018; Gross and Canteras, 2012; Shang et
390 al., 2015; Wang et al., 2015), relatively simple neural circuits mediate the escape
391 behavior in fish and invertebrates (Card, 2012; Eaton et al., 2001). In such simple neural
392 systems that mediate escape behavior, a few neurons have been identified that trigger
393 the escape responses to a specific sensory stimulus which indicate the predator's
394 approach. In flies, a key set of neurons called giant fibers directly induce quick
395 taking-off as an escape response (Allen et al., 2006). To choose from two types of
396 escaping take-off depending on the stimulus velocity, the presence of neural circuits in
397 which specific projection neurons provide information of stimulus velocity to the giant
398 fiber have been proposed in the fly (von Reyn et al., 2014, 2017). In context, our results

399 show that crickets choose escape responses based on multiple stimulus parameters for
400 the first time, which would promote an understanding of the mechanism of choosing
401 appropriate behavior according to varied situations in the natural field.

402 The neural basis of the cercal sensory system to process airflow information,
403 which in turn mediates wind-elicited escape behavior, has been well studied (Jacobs et
404 al., 2008; Baba and Ogawa, 2017). Air currents are detected as air-particle displacement
405 by filiform hairs on the cerci (Miller et al., 2011; Shimozawa and Kanou, 1984), and
406 several wind-sensitive interneurons, including giant interneurons (GIs), which have
407 been identified as ascending projection neurons, receive excitatory synaptic inputs from
408 the sensory afferents of the mechanoreceptor neurons of the hair sensilla. The GIs
409 encode various characteristics of the surrounding air currents such as velocity, direction,
410 and frequency in their firing activity (Aldworth et al., 2011; Miller et al., 1991), and
411 project their long axons through the ventral nerve cord to higher centers, including the
412 thoracic ganglia and the brain (Hirota et al., 1993). Because the GIs differs from each
413 other in their sensitivities to the direction and intensity of the air currents (Jacobs et al.,
414 2008; Miller et al., 1991; Ogawa et al., 2008), the GIs likely provide distinct sensory
415 information to their postsynaptic partners. Thus, further investigation of the
416 postsynaptic circuit of GIs would clarify the neural mechanism underlying action
417 selection depending on the multiple stimulus parameters.

418

419 **Stimulus characteristics that were likely to elicit jumping**

420 The faster and longer the air currents, the more frequently the jumping response was
421 elicited. This is due to the velocity and duration of the air-current stimulus being
422 considered to be correlated with the size of the predator and their approaching speed

(Casas and Dangles, 2010), crickets would choose to jump in situations where a larger predator attacked them more quickly. It should be noted, however, that the jumping probability was saturated at approximately 50% even for the fastest and longest stimulus, which was the most inducible for the jump (Fig. 1). One possibility is that additional sensory inputs may be required to further elevate the likelihood of jumping selection. Animals use a variety of sensory modalities to detect predators. For example, auditory stimuli combined with air currents alter the contents of escape responses in crickets (Fukutomi and Ogawa, 2017; Fukutomi et al., 2015). Even if they do not directly elicit escape responses, other sensory inputs that inform external contexts or internal conditions of the animals affect the escape responses (Domenici et al, 2008; Matsuura et al., 2002). Therefore, crickets may jump more frequently than 50% in different contexts or situations.

In contrast, the stimulus angle did not significantly affect the selection of running and jumping. This result is consistent with a previous report where crickets have the same accuracy of directional controllability during running and jumping (Sato et al., 2019). In this study, a strong correlation, which could be approximated by $y = x$, between the movement direction and stimulus angle, was also observed in the velocity test (Fig. 5) and the duration test (Fig. 6). These results indicated that the escape direction could be controlled against the stimulus angle in either type of escape response, independent of the stimulus velocity and duration. It is supposed that the sensory information of the stimulus angle would be conveyed by neural channels different from those for stimulus velocity and duration.

445

446 **Stimulus dependency of the locomotion performance**

447 The crickets changed their moving speed and travel distance according to the stimulus
 448 parameters during running, but not during jumping. This locomotion controllability is
 449 the behavioral advantage of running compared to jumping. In contrast, the invariance of
 450 the jumping speed and distance to the stimulus parameters illustrated that jumping was a
 451 more stereotyped response, which might be more predictable for predators. These
 452 results are consistent with our previous reports that running is a more flexible response
 453 during which crickets respond to the additional stimulus, compared to jumping (Sato et
 454 al., 2019).

455 Interestingly, the reaction time decreased as the stimulus velocity increased
 456 during both running and jumping (Fig. 3C). Previous studies have demonstrated that the
 457 escape responses to visual looming stimuli start at a specific angular size of the stimulus,
 458 which indicates the distance to the stimulus. This suggests that the distance to the
 459 predators, rather than the speed of the predator's approach, is a more crucial sensory cue
 460 for the prey to decide an escape start (Bhattacharyya et al., 2017; Dunn et al., 2016;
 461 Fotowat and Gabbiani, 2007). In contrast, our results revealed a strong relationship
 462 between stimulus velocity and escape latency. This means that the crickets may decide
 463 to start escaping based on the stimulus velocity, which indicates the approaching speed
 464 of a predator. The faster a predator approaches, the less time it takes to reach its prey;
 465 thus, the reaction time is important for the prey to increase the success rate of the escape
 466 behavior (von Reyn et al., 2014; Walker et al., 2005). In particular, when animals of
 467 prey cannot visually detect the predator's approach, as in the dark, they will make
 468 decisions regarding the escape start based on the stimulus velocity for effective survival.

469 Unlike the metric locomotor parameters, the movement direction was
 470 accurately controlled almost independent of velocity or duration of the stimulus. This

471 result was consistent with a previous study reporting that the direction of the escape
 472 running on a treadmill is similarly controlled to stimuli of different durations (Oe and
 473 Ogawa, 2013). The accuracy of directional control decreased only in the running
 474 response to the shortest stimulus (left in Fig. 6B). There is a possibility that a 20 ms
 475 stimulus is too short for the crickets to perceive their direction. This is also supported by
 476 the result where the reaction time for running response to the shortest stimulus was
 477 longer than that for stimuli with longer durations (left in Fig. 4C). Air currents longer
 478 than a certain duration will likely be necessary for the cricket to perceive stimulus
 479 orientation for directional control of the escape response.
 480

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489 Formal analysis: N.S.; Investigation: N.S.; Data curation: N.S.; Writing – original draft:

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497 **REFERENCES**

- 498 **Aldworth, Z.N., Dimitrov, A.G., Cummins, G.I., Gedeon, T. and Miller, J.P.** (2011).
 499 Temporal encoding in a nervous system. *PLoS Comput. Biol.* **7**, e1002041.
- 500 **Allen, M. J., Godenschwege, T. A., Tanouye, M. A. and Phelan, P.** (2006). Making
 501 an escape: Development and function of the *Drosophila* giant fibre system. *Semin.*
 502 *Cell Dev. Biol.* **17**, 31–41.
- 503 **Baba, Y. and Ogawa, H.** (2017). Cercal system-mediated antipredator behaviors. In
 504 *The cricket as a model organism* (ed. H.W. Horsch, T. Mito, A. Popadic, H. Ohuchi,
 505 and S. Noji), pp. 211–228. Springer.
- 506 **Baba, Y. and Shimozawa, T.** (1997). Diversity of motor responses initiated by a wind
 507 stimulus in the freely moving cricket, *Gryllus bimaculatus*. *Zool. Sci.* **14**, 587–594.
- 508 **Bhattacharyya, K., McLeen, D. L. and MacIver, M. A.** (2017). Visual threat
 509 assessment and reticulospinal encoding of calibrated responses in larval zebrafish.
 510 *Curr. Biol.* **27**, 2751–2762.
- 511 **Briggman, K. L., Abarbanel, H. D. and Kristan, W. B.** (2005). Optical imaging of
 512 neuronal populations during decision-making. *Science* **307**, 896–901.
- 513 **Bulbert, M. W., Page, R. A. and Bernal, X. E.** (2015). Danger comes from all fronts:
 514 predator-dependent escape tactics of túngara frogs. *PLoS ONE* **10**, e0120546.
- 515 **Card, G. M.** (2012). Escape behaviors in insects. *Curr. Opin. Neurobiol.* **22**, 180–186.
- 516 **Card, G. and Dickinson, M.** (2008). Performance trade-offs in the flight initiation of
 517 *Drosophila*. *J. Exp. Biol.* **211**, 341–353.
- 518 **Casas, J. and Dangles, O.** (2010). Physical ecology of fluid flow sensing in arthropods.
 519 *Annu. Rev. Entomol.* **55**, 505–520.
- 520 **Dangles, O., Ory, N., Steinmann, T., Christides, J.-P. and Casas, J.** (2006).

521 Spider' s attack versus cricket' s escape: velocity modes determine success. *Anim.*
522 *Behav.* **72**, 603–610.

523 **De Franceschi, G., Vivattanasam, T., Saleem, A. B. and Solomon, S. G.** (2016).
524 Vision guides selection of freeze or flight defense strategies in mice. *Curr. Biol.* **26**,
525 2150–2154.

526 **Domenici, P.** (2010). Context-dependent variability in the components of fish escape
527 response: integrating locomotor performance and behavior. *J. Exp. Zoo.* **313A**,
528 59–79.

529 **Domenici, P., Blagburn, J. H. and Bacon, J. P.** (2011a). Animal escapology I:
530 theoretical issues and emerging trends in escape trajectories. *J. Exp. Biol.* **214**,
531 2463–2473.

532 **Domenici, P., Blagburn, J. M. and Bacon, J. P.** (2011b). Animal escapology II: escape
533 trajectory case studies. *J. Exp. Biol.* **214**, 2474–2494.

534 **Domenici, P., Booth, D., Blagburn, J. M. and Bacon, J. P.** (2008). Cockroaches keep
535 predators guessing by using preferred escape trajectories. *Curr. Biol.* **18**,
536 1792–1796.

537 **Dunn, T. W., Gebhardt, C., Nauman, E. A., Riegler, C., Ahrens, M. B., Engert, F.**
538 **and Del Bene, F.** (2016). Neural circuits underlying visually evoked escapes in
539 larval zebrafish. *Neuron* **89**, 613–628.

540 **Dupuy, F., Casas, J., Body, M. and Lazzari, C. R.** (2011). Danger detection and
541 escape behaviour in wood crickets. *J. Insect Physiol.* **57**, 865–871.

542 **Eaton, R. C., Lee, R. K. K. and Foreman, M. B.** (2001). The Mauthner cell and other
543 identified neurons of the brainstem escape network of fish. *Prog. Neurobiol.* **63**,
544 476–485.

545 **Eilam, D.** (2005). Die hard: a blend of freezing and fleeing as a dynamic
546 defense—implications for the control of defensive behavior. *Neurosci. Biobehav. Rev.*
547 **29**, 1181–1191.

548 **Evans, D. A., Stempel, A. V., Vale, R. and Branco, T.** (2019). Cognitive control of
549 escape behaviour. *Trends Cogn. Sci.* **23**, 334–348.

550 **Evans, D. A., Stempel, A. V., Vale, R., Ruehle, S., Lefler, Y. and Branco, R.** (2018). A
551 synaptic threshold mechanism for computing escape decisions. *Nature* **558**,
552 590–594.

553 **Fadok, J. P., Krabbe, S., Markovic, M., Courtin, J., Xu, C., Massi, L., Botta, P.,**
554 **Bylund, K., Müller, C., Kovacevic, A., et al.** (2017). A competitive inhibitory
555 circuit for selection of active and passive fear responses. *Nature* **542**, 96–100.

556 **Fotowat, H. and Gabbiani, F.** (2007). Relationship between the phases of sensory and
557 motor activity during a looming-evoked multistage escape behavior. *J. Neurosci.* **27**,
558 10047–10059.

559 **Fukutomi, M. and Ogawa, H.** (2017). Crickets alter wind-elicited escape strategies
560 depending on acoustic context. *Sci Rep.* **7**, 15158.

561 **Fukutomi, M., Someya, M. and Ogawa, H.** (2015). Auditory modulation of
562 wind-elicited walking behavior in the cricket *Gryllus bimaculatus*. *J. Exp. Biol.* **218**,
563 3968–3977.

564 **Gross, C. T. and Canteras, N. S.** (2012). The many path to fear. *Nature Rev. Neurosci.*
565 **13**, 651–658.

566 **Hirota, K., Sonoda, Y., Baba, Y. and Yamaguchi, T.** (1993). Distinction in
567 morphology and behavioral role between dorsal and ventral groups of cricket giant
568 interneurons. *Zool. Sci.* **10**, 705–709.

569 **Jacobs, G. A., Miller, J. P. and Aldworth, Z.** (2008). Computational mechanisms of
570 mechanosensory processing in the cricket. *J. Exp. Biol.* **205**, 2005–2016.

571 **LeDoux, J. and Daw, N. D.** (2018). Surviving threats: neural circuit and computational
572 implications of a new taxonomy of defensive behavior. *Nat. Rev. Neurosci.* **19**,
573 269–282.

574 **Liu, Y. C. and Hale, M. E.** (2017). Local spinal cord circuits and bilateral Mauthner
575 cell activity function together to drive alternative startle behaviors. *Curr. Biol.* **27**,
576 697–704.

577 **Matsuura, T., Kanou, M. and Yamaguchi, T.** (2002). Motor program initiation and
578 selection in crickets, with special reference to swimming and flying behavior. *J.*
579 *Comp. Physiol. A* **187**, 987–995.

580 **Miller, J. P., Jacobs, G. A. and Theunissen, F. E.** (1991). Representation of sensory
581 information in the cricket cercal sensory system. I. Response properties of the
582 primary interneurons. *J. Neurophysiol.* **66**, 1680–1689.

583 **Miller, J. P., Krueger, S., Heys, J. J. and Gedeon, T.** (2011). Quantitative
584 characterization of the filiform mechanosensory hair array on the cricket cercus.
585 *PLoS ONE* **6**, e27873.

586 **Oe, M. and Ogawa, H.** (2013). Neural basis of stimulus-angle-dependent motor control
587 of wind-elicited walking behavior in the cricket *Gryllus bimaculatus*. *PLoS ONE* **8**,
588 e80184.

589 **Ogawa, H., Cummins, G. I., Jacobs, G. A. and Oka, K.** (2008). Dendritic design
590 implements algorithm for synaptic extraction of sensory information. *J. Neurosci.*
591 **28**, 4592–4603.

592 **Preuss, T., Osei-Bonsu, P. E., Weiss, S. A., Wang, C. and Fabor, D. S.** (2006). Neural

593 representation of object approach in a decision-making motor circuit. *J. Neurosci.*
594 **26**, 3454–3464.

595 **Santer, R. D., Yamazaki, Y., Rind, F. C. and Simmons, P. J.** (2005). Motor activity
596 and trajectory control during escape jumping in the locust *Locusta migratoria*. *J.*
597 *Comp. Physiol. A.* **191**, 965–975.

598 **Sato, N., Shidara, H. and Ogawa, H.** (2017). Post-molting development of
599 wind-elicited escape behavior in the cricket. *J. Insect. Physiol.* **103**, 36–46.

600 **Sato, N., Shidara, H. and Ogawa, H.** (2019). Trade-off between motor performance
601 and behavioural flexibility in the action selection of cricket escape behaviour. *Sci*
602 *Rep* **9**, 18112.

603 **Shang, C., Liu, Z., Chen, Z., Shi, Y., Wang, Q., Liu, S., Li, D. and Cao, P.** (2015). A
604 parvalbumin-positive excitatory visual pathway to trigger fear responses in mice.
605 *Science* **348**, 1472–1477.

606 **Shimozawa, T. and Kanou, M.** (1984). Varieties of filiform hairs: range fractionation
607 by sensory afferents and cercal interneurons of a cricket. *J. Comp. Physiol. A* **155**,
608 485–493.

609 **Simmons, P. J., Rind, F. C. and Santer, R. D.** (2010). Escapes with and without
610 preparation: The neuroethology of visual startle in locusts. *J. Insect Physiol.* **56**,
611 876–883.

612 **Stewart, W. J., Cardenas, G. S. and McHenry, M. J.** (2013). Zebrafish larvae evade
613 predators by sensing water flow. *J. Exp. Biol.* **216**, 388–398.

614 **Takagi, S., Cocanougher, B. T., Niki, S., Miyamoto, D., Kohsaka, H., Kazama, H.,**
615 **Fetter, R. D., Truman, J. W., Zlatic, M., Cardona, A., et al.** (2017). Divergent
616 connectivity of homologous command-like neurons mediates segment-specific

617 touch responses in *Drosophila*. *Neuron* **96**, 1373–1387.

618 **Turner, H. N., Amengol, K., Patel, A. A., Himmel, N. J., Sullivan, L., Iyer, S. C.,**
619 **Bhattacharyya, S., Iyer, E. P. R., Landry, C., Galko, M. J., et al.** (2016). The
620 TRP channels Pkd2, NompC, and Trpm act in cold-sensing neurons to mediate
621 unique aversive behaviors to noxious cold in *Drosophila*. *Curr. Biol.* **26**,
622 3116–3128.

623 **von Reyn, C. R., Breads, P., Peek, M. Y., Zheng, G. Z., Williamson, W. R., Yee, A.**
624 **L., Leonardo, A. and Card, G. M.** (2014). A spike-timing mechanism for action
625 selection. *Nat. Neurosci.* **17**, 962–970.

626 **von Reyn, C. R., Nern, A., Williamson, W. R., Breads, P., Wu, M., Namiki, S. and**
627 **Card, G. M.** (2017). Feature integration drives probabilistic behavior in the
628 drosophila escape response. *Neuron* **94**, 1190–1204.

629 **Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenny, D. and Reznik, D. N.**
630 (2005). Do faster starts increase the probability of evading predators? *Funct. Ecol.*
631 **19**, 808–815.

632 **Wang, L., Chen, I. Z. and Lin, D.** (2015). Collateral pathways from the ventromedial
633 hypothalamus mediate defensive behaviors. *Neuron* **85**, 1344–1358.

634 **Watanabe, T., Ugajin, A. and Aonuma, H.** (2018). Immediate-early promoter-driven
635 transgenic reporter system for neuroethological research in a hemimetabolous
636 insect. *eNeuro* **5**.

637

638 **Figure legends**

639 **Fig. 1. Effects of three stimulus parameters on action selection of running and**
640 **jumping. (A)** Distribution of the response probability against the stimulus angle in the
641 angle test. Left diagram shows the definition of the stimulus angle. Right histograms
642 represent the ratio of the number of responses to the number of trials for a range of
643 every 20 degree of the stimulus angles. The air current with a velocity of 834 mm s^{-1}
644 and a duration of 200 ms was used. $N=10$ animals. **(B)** The selection ratio of running
645 (blue) to jumping (red) in the angle test. The data is shown in four divisions based on
646 the absolute value of the stimulus angle. **(C)** Changes in the response probability over
647 the stimuli with different velocities. Left diagram indicates four types of stimuli used in
648 the velocity test, in which velocity was varied and duration was fixed to 200 ms. $N=10$
649 animals. **(D)** The selection ratio of running (blue) to jumping (red) in the velocity test.
650 **(E)** Changes in the response probability over the stimuli with different durations. Left
651 diagram indicates five types of stimuli used in the duration test, in which duration was
652 varied and velocity was fixed to 834 mm s^{-1} . $N=10$ animals. **(F)** The selection ratio of
653 running (blue) to jumping (red) in the duration test. In (C) and (E), gray open circles
654 connected with gray lines represent the probability for each individual, and black filled
655 circles represent the mean of the individuals' probability, for each velocity or duration
656 of stimuli. *** $P<0.001$, N.S. not significant, coefficients for each of the stimulus
657 parameter in logistic regression analysis.

658

659 **Fig. 2. Effects of stimulus angle on metric locomotor parameters. (A–C)**

660 Relationships between the stimulus angle and the movement distance (A), maximum
661 translational velocity (B), or reaction time (C), in running (left) and jumping (right) in

the angle test. The velocity and duration of air current were fixed to 834 mm s⁻¹ and 200 ms, respectively. The total number of responses used for the analysis were 106 and 76 for running and jumping, respectively. Lines indicate the regression lines with a significant slope. **P*<0.05, ***P*<0.01, N.S. not significant, linear regression analysis. *N*=10 animals.

Fig. 3. Effects of stimulus velocity on metric locomotor parameters. (A–C) The movement distance (A), maximum translational velocity (B), and reaction time (C), in running (left) and jumping (right). The total number of responses used for the analysis were 56, 101, 98 and 84 for running, and 7, 51, 81 and 100 for jumping, for 340, 618, 734 and 834 mm s⁻¹ for stimulus velocities, respectively. Colored filled circles represent the data for each trial and black open circles represent the mean of the data in all trials for each velocity of stimuli. ***P*<0.01, ****P*<0.001, N.S. not significant, likelihood ratio test for LMMs. *N*=10 animals.

Fig. 4. Effects of stimulus duration on metric locomotor parameters. (A–C) The movement distance (A), maximum translational velocity (B), and reaction time (C), in running (left) and jumping (right). The total number of responses used for the analysis were 39, 101, 88, 90 and 85 of running, and 0, 33, 87, 97 and 98 of jumping, for 20, 40, 60, 80 and 100 ms of stimulus durations, respectively. Colored filled circles represent the data for each trial and black open circles represent the mean of the data in all trials for each duration of stimuli. No jumping was elicited by the stimulus of 20-ms duration. ****P*<0.001, N.S. not significant, likelihood ratio test for LMMs. *N*=10 animals.

686 **Fig. 5. Effects of stimulus velocity on directional control.** (A) Relationships between
 687 the movement direction and stimulus angle in running (blue) and jumping (red), for the
 688 stimuli of different velocities, 340, 618, 734, and 834 mm s⁻¹. Colored lines represent
 689 linear regression lines with a significant slope for the data of running (blue) and
 690 jumping (red), respectively. Black dotted lines indicate the line of $y = x$. (B) Absolute
 691 values of the angular difference between the movement direction and stimulus angle in
 692 running (left) and jumping (right). Colored filled circles represent the data for each trial
 693 and black open circles represent the mean of the data in all trials, for each velocity of
 694 stimuli. N.S. not significant, likelihood ratio test for LMMs. $N=10$ animals.

695
 696 **Fig. 6. Effects of stimulus duration on directional control.** (A) Relationships between
 697 the movement direction and stimulus angle in running (blue) and jumping (red), for the
 698 stimuli of different durations, 20, 40, 60, 80, and 100 ms. No jumping was elicited by
 699 the 20 ms duration stimulus. Colored lines represent linear regression lines with a
 700 significant slope for the data of running (blue) and jumping (red), respectively. Black
 701 dotted lines indicate the line of $y = x$. (B) Absolute values of the angular difference
 702 between movement direction and stimulus angle in running (left) and jumping (right).
 703 Colored filled circles represent the data for each trial and black open circles represent
 704 the mean of the data in all trials, for each duration of stimuli. $**P<0.01$, N.S. not
 705 significant, likelihood ratio test for LMMs. $N=10$ animals.

706

707 **Tables**

708 **Table 1. Results of multiple logistic regression analysis to test the effect of stimulus**
 709 **parameters and trial order on the response probability and selected ratio.**

Experiment	Parameter	Explanatory variable	Result of logistic regression		
			Coefficient	z value	p value
“angle test”	Selection ratio	Stimulus angle	-0.269	-1.841	0.066
	(Fig. 1B)	Trial order	-0.002	-0.083	0.934
“velocity test”	All probability	Stimulus velocity	0.008	13.81	<0.001
	(Fig. 1C)	Trial order	-0.015	-0.882	0.378
	Selection ratio	Stimulus velocity	0.004	5.896	<0.001
	(Fig. 1D)	Trial order	0.003	0.185	0.853
“duration test”	All probability	Stimulus duration	0.072	14.57	<0.001
	(Fig. 1D)	Trial order	-0.014	-0.865	0.387
	Selection ratio	Stimulus duration	0.023	6.722	<0.001
	(Fig. 1F)	Trial order	0.006	0.473	0.636

710

711

Table 2. Results of linear regression analysis to test the relationships between the metric locomotor parameters and stimulus angle.

Parameter	Response	Result of linear regression		
		Estimated slope	t value	p value
Movement distance (Fig. 2A)	Running	-0.104	-3.346	0.001
	Jumping	-0.073	-1.213	0.229
Max. velocity (Fig. 2B)	Running	-0.360	-2.160	0.033
	Jumping	0.652	2.105	0.039
Reaction time (Fig. 2C)	Running	0.140	3.076	0.003
	Jumping	0.021	0.545	0.587

Table 3. Results of likelihood ratio test for LMMs to test the effects of stimulus velocity and duration on the locomotor parameters.

Experiment	Parameter	Response	Result of likelihood ratio test	
			Chi-squared	p value
Velocity test	Movement distance (Fig. 3A)	Running	9.287	0.002
		Jumping	0.254	0.614
	Max. velocity (Fig. 3B)	Running	22.10	<0.001
		Jumping	0.035	0.851
	Reaction time (Fig. 3C)	Running	254.7	<0.001
		Jumping	149.6	<0.001
	Directional accuracy (Fig. 5B)	Running	0.3176	0.573
		Jumping	0.530	0.467
Duration test	Movement distance (Fig. 4A)	Running	17.24	<0.001
		Jumping	2.284	0.131
	Max. velocity (Fig. 4B)	Running	74.93	<0.001
		Jumping	0.785	0.376
	Reaction time (Fig. 4C)	Running	36.20	<0.001
		Jumping	3.431	0.064
	Directional accuracy (Fig. 6B)	Running	7.681	0.006
		Jumping	0.787	0.375

Table 4. Summary of the result of linear regression analysis for the movement direction and stimulus angle in “velocity test” and “duration test” experiments.

Experiment	Stimulus parameter		Response	Significance of coefficient		
	Velocity	Duration		Estimated slope	t value	p value
“velocity test” (Fig. 5A)	340 mm s ⁻¹	200 ms	Running	0.938	17.65	<0.001
			Jumping	0.479	1.864	0.121
	618 mm s ⁻¹	200 ms	Running	0.868	24.42	<0.001
			Jumping	0.986	21.61	<0.001
	734 mm s ⁻¹	200 ms	Running	0.968	31.46	<0.001
			Jumping	0.910	26.45	<0.001
	834 mm s ⁻¹	200 ms	Running	0.909	26.44	<0.001
			Jumping	0.981	32.84	<0.001
	834 mm s ⁻¹	20 ms	Running	0.946	9.727	<0.001
			Jumping	-	-	-
“duration test” (Fig. 6A)	834 mm s ⁻¹	40 ms	Running	0.934	23.49	<0.001
			Jumping	1.015	14.66	<0.001
	834 mm s ⁻¹	60 ms	Running	0.930	23.84	<0.001
			Jumping	0.938	25.05	<0.001
	834 mm s ⁻¹	80 ms	Running	0.987	23.48	<0.001
			Jumping	0.908	24.81	<0.001
	834 mm s ⁻¹	100 ms	Running	1.002	25.63	<0.001
			Jumping	0.965	32.33	<0.001

Fig 1

Fig 2

Fig 3

A

B

C

Fig 4

A

B

C

Fig 5

A

B

Fig 6