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Evaluation of Visual and Tactile Perception by Plain-body Octopus (*Callistoctopus aspilosomatis*) of Prey-like Objects

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We investigated the characteristic features of perception in octopuses by examining multisensory information from an object simulating prey, which provided different visual and tactile stimuli. In experiments, we presented plain-body octopus with four kinds of models, namely, the Lifelike crab, the Embedded crab, the Translucent crab, and the Black cuboid. These models contain different amounts of visual and tactile information that a crab originally contains: the Lifelike crab resembles a crab both visually and tactilely, the Embedded crab resembles a crab visually but provides different tactile information, the Translucent crab provides tactile information of a crab but contains less visual information, and the Black cuboid lacks both visual and tactile information of a crab. Among these four models, octopuses contacted most with the Lifelike crab, which was similar to their behavior with a crab. Indeed, octopuses were fastest to contact the Lifelike crab and had the longest duration of contacting it among the four models. Octopuses contacted the Embedded crab more than the Translucent crab, both of which had contrasting visuo-tactile information compared to that of a crab. Quickness of octopuses to contact and duration of contact with the Embedded crab were more similar to those with the Lifelike crab than to those with the Translucent crab. Furthermore, octopuses contacted the Black cuboid least among the models. These results suggest that octopuses compositely detect both visual and tactile information in order to perceive an object. Furthermore, octopuses possess the potential priority either for visual or tactile information, by which they process the target object.

Key words: behavior, cephalopod, crab, octopus, visuo-tactile perception

INTRODUCTION

Coleoid cephalopods (octopuses, cuttlefishes, and squids), a group of mollusks, have developed a nervous system in their entire body (ca. 500 million neurons), which is centralized in the head region to form a brain, which is equivalently as large as a vertebrate's brain (Packard, 1972). Cephalopods also possess sophisticated sensory organs such as lens eyes similar to our own (Budelmann, 1994). Due to these biological features, cephalopods exhibit unique behaviors that involve neural control, such as a high level of learning and memory, and body patterning with suddenly changing chromatic and textural forms for camouflage and communication (Hanlon and Messenger, 1996).

In a cephalopod brain, the optic lobe, a region involved in visual processing, is the largest structure (Young, 1963), which assures a high level of visual abilities of cephalopods (Hanlon and Messenger, 1996). On the other hand, cephalopods are equipped with other sensory organs such as skin and suckers that receive tactile information (the suckers also perceive taste) (Wells, 1978). These sense organs might enable cephalopods to receive multisensory information from their surroundings. Among cephalopods, octopuses have been the most studied subjects for this topic and have been examined for different types of learning abilities. For example, common octopus (*Octopus vulgaris*) can visually discriminate objects that differ in shape, size, orientation (Boycott and Young, 1956; Sutherland, 1962; Sutherland et al., 1963), and brightness (Messenger et al., 1973). Also, they can tactilely discriminate objects that differ in curvature and roughness (Wells and Wells, 1957; Wells, 1964). In terms of dependence on different senses, there exists variation among cephalopods, which can be seen in brain anatomy in regions that process tactile inputs, such as subfrontal and inferior frontal lobes; these regions are larger in octopuses than in squids and cuttlefishes (Young, 1988). This difference is also reflected in their behaviors, as octopuses exhibit a benthic mode of life in which arms (entrance of tactile inputs) are frequently used for hunting and foraging (Young, 1988).

In general, animals live in an environment in which different types of sensory inputs, namely, color, shape, sound, texture, and taste, occur. In this situation, it should be adaptive for animals to integrate the different sensory information that they perceive for making decisions instantly in their behaviors such as escape, attack, or mate. Actually, sensory integration is commonly seen in a wide range of ani-

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mals. For example, integration of visual and tactile information (visuo-tactile) has been observed in humans (Gaydos, 1956), keas (*Nestor notabilis*) (Carducci et al., 2018), capuchin monkeys (*Cebus paella*) (Carducci et al., 2018), and bumble bees (*Bombus terrestris*) (Solvi et al., 2020). Other combinations of sensory integration have also been observed, such as visual and auditory information in rats (Sheppard et al., 2013) and visual and electric information in elephant nose fish (*Gnathonemus petersii*) (Schumacher et al., 2016). These sensory integrations do not reflect phylogenetic background but are clearly related to the behavioral characteristics and life mode of each species studied. Based on the multisensory system of octopuses, it is likely that this animal also integrates different sensory inputs from its surroundings. Some studies have shown that octopuses simultaneously compile sensory input through their complex behavior. For instance, visual information (black or white) was shown to interact with tactile information (rough or smooth) in the object discrimination tasks of some octopus species (*Octopus maya*, *O. vulgaris*, *Octopus bimaculatus* [Allen et al., 1986] and *Octopus diguetid* [Michels et al., 1987], but not in *O. vulgaris* or *O. bimaculatus* (Michels et al., 1987). The observation that *O. vulgaris* detects visual information to determine the direction of its arm movement to grasp a food reward (Gutnick et al., 2011) also suggests that octopuses can integrate visual and somatosensory information to control their movement. However, no studies have focused on whether there is a priority between the multisensory inputs of the octopus. In addition, the effects of these different types of sensory information on the octopuses' behavior are unknown, except for a few examples, such as those seen in *O. vulgaris*, in which chemical information precedes visual information regarding food choice (Maselli et al., 2020). This lack of knowledge about the sensory properties for perception may be partially because much of the physiological and psychological research interest in octopuses has regarded vision, which can perceive the world with human-like eyes (Wells, 1963), which is unique from an evolutionary perspective. In addition, it might be difficult to set a suitable experimental paradigm in octopuses for testing other senses besides vision, and to set a method to test for multisensory integration, in which different sensory inputs are usually mixed.

Based on this background, we investigated whether there is a priority between visual and tactile sensory inputs when the octopus detects a specific object with an uneven form. For this purpose, we chose plain-body octopus (*Callistoctopus aspilosomatis*), which inhabits the coastal tropical waters of the Ryukyu Archipelago, because we have succeeded in training this octopus to learn a specific object visually and tactilely (Kawashima et al., 2021). In a previous study, we confirmed that octopuses refer to visual information as well as tactile information from a novel object (a white cross in that case) to judge its image, which tentatively suggested the occurrence of multisensory integration in this octopus species (Kawashima et al., 2021). A similar suggestion was also obtained from operant conditioned prickly octopus (*Abdopus aculeatus*), which also inhabits the tropical coastal waters of the Ryukyu Archipelago (Kawashima et al., 2020). Furthermore, field observations of octopuses have shown that they use both visual and tactile sensory input for hunting. For example, the big blue octopus (*Octopus cyanea*) visually attacks prey, but applies a tactile approach when the prey is not visible, such as when it is hiding under rocks (Forsythe and Hanlon, 1996). These examples indicate that the feeding behavior is the most useful to observe for examining the visual and tactile perception of the octopus. In the current study, we presented different types of objects that contained different amounts of sensory information of the subtropical pebble crab *Gaetice depressus*, a species that the plain-body octopus prefers to feed on, as other crabs are fed upon by many octopuses (Boletzky and Hanlon, 1983). Because we often encounter *C. aspilosomatis* that feeds on *G. depressus* in nature (Kawashima, personal observation), it can be believed that octopuses already have the sensory information such as form, texture, and chromatic patterns of this crab. Therefore, octopuses are very likely to have already built their own sensory image of the crab. Based on this idea, we presented octopuses with some models of the crab that produced different sensory inputs to octopuses, and observed how octopuses behaved toward these different target objects.

MATERIALS AND METHODS

Collection and maintenance of animals

Six individuals of *C. aspilosomatis* were collected from the coastal waters of Okinawa Island, the Ryukyu Archipelago, Japan. Immediately after capture, these individuals were placed in a bucket of aerated seawater. These octopuses were then transported to the laboratory of the Faculty of Science, University of the Ryukyus, at Nishihara campus. Upon arrival, these octopuses were transferred to separate cubic tanks (20 L, 300-mm square) of a closed seawater system with filtration, where they were reared throughout the study. The walls of the tanks were covered with black plastic board to decrease the stress experienced by the octopuses. Coral gravel was placed on the entire bottom of the aquarium (depth 10 mm), and water depth was set to 250 mm. We used artificial seawater (TetraMarine Salt Pro, Tetra, Blacksburg, Virginia, USA) and it was maintained throughout the study at 25.0 ± 1°C, 34.00 ± 2 ppt, and pH 7.8–8.2. Octopuses were usually fed once a day between 5:30–9:00 with frozen giant tiger prawn, *Penaeus monodon*, and subtropical pebble crab *Gaetice depressus*. After octopuses were tested for the behavioral experiments, each octopus was euthanized by placing it in seawater with 10% ethanol, and then dissected to determine sex, dorsal mantle length, wet body weight, and maturity (Table 1).

Experiment

After 2 to 10 weeks of rearing, octopuses became acclimated to the conditions in the laboratory, and once they started to feed on the prey provided in a positive manner, we started the behavioral experiments with them. Because of this situation, the starting date for experiments differed among individuals.

We chose a crab as a stimulus model, because a crab decoy (single size and color pattern) can induce attack by *O. vulgaris*, which is applicable as a test for assessing the health condition of octopuses (Amodio et al., 2014). In this study, we presented separately four types of models that did or did not simulate the subtropical pebble crab to octopuses. These were the Lifelike crab (Fig. 1A), the Embedded crab (Fig. 1B), the Translucent crab (Fig. 1C) and the Black cuboid (a control) (Fig. 1D). These models were made as follows. We caught live subtropical pebble crabs from coastal waters of Okinawa Island, the Ryukyu Archipelago, and euthanized them in a freezer. Then, we made casts of these crabs using silicon and made plastic models from these casts by introducing translucent epoxy resin in the casts. These plastic models were colored with

Table 1. Summary of individual information of six plain-body octopus *Callistoctopus aspilosomatis* that were collected from the coastal waters of Okinawa-jima Island, the Ryukyu Archipelago, Japan, and used in the experiments. After the experiments were completed, the dorsal mantle length (ML), wet body weight (BW), sex, and maturation of octopuses were measured and determined.

Individual ID	Date of collection	Date of death	ML (mm)	BW (g)	Sex	Maturation
A	21 Mar. 2020	23 Sep. 2020	60	93.4	F	immature
B	9 Jan. 2020	31 Aug. 2020	50	48.8	F	immature
C	6 Apr. 2020	25 Sep. 2020	70	68.72	F	maturing
D	21 Mar. 2020	20 Aug. 2020	55	53.52	M	mature
E	6 Apr. 2020	25 Sep. 2020	45	30.92	F	immature
F	6 Apr. 2020	24 Nov. 2020	45	23.18	M	mature

paint. Finally, these models looked like genuine crabs and provide almost identical visual and tactile information to that of a crab. Using this method, we made four types of models with two colors (green and black, common colors of these crabs encountered in nature) and two sizes (large and small, resembling genuine crabs) (Fig. 1A). We made these chromatic and size variations to avoid a situation in which the octopuses learn or are accustomed to the specific characteristics of a model. The second model, the Embedded crab, was a model of a crab that was embedded in transparent plastic. This model was made similarly to the first model (the Lifelike crab) and then embedded in a cubic form with epoxy resin. The Embedded crab therefore provides visual information similar to a crab but not tactile information of a crab. We made four embedded models with two colors (green and black) and two sizes (large and small), similar to the Lifelike crabs (Fig. 1B). The third model, the Translucent crab, was a model of a colorless crab (i.e., the first model [the Lifelike crab] without coloration). This model was made in the same way as the first model but was not colored. The Translucent crab therefore provides tactile information similar to a crab but lacks visual information of a crab except for its outline. We made two translucent models with two sizes (large and small, the same as the Lifelike crab) (Fig. 1C). The fourth model, the Black cuboid, was a black cube that was made by introducing epoxy resin into a cubic form (Fig. 1D). The black plastic cuboid provides no information of a crab, and therefore was used as a control for the remaining three models described above.

We presented these four models to octopuses once a day and each presentation took 10 minutes. When we presented the model to an octopus in an aquarium, we first put a gray blindfold board (50 mm × 50 mm) in the aquarium using a pair of tweezers with one of the four models behind the board (Fig. 1E). We then removed the blindfold board, and left the model to be presented to the octopus (Fig. 1E). All four models were presented to the octopus in a random order, including variations of a single model (color and size). When the octopus attempted to contact a model, we allowed it to move by itself toward the model. After the experiment, we presented a defrosted crab to the octopus to confirm the presence of feeding motivation. If the octopus did not feed on the crab presented within 10 minutes, we regarded that the individual lacked feeding motivation, and excluded the data of that day from our analysis. We repeated this experiment for consecutive days until countable results were achieved 20 times for each of the four models. The days taken by octopuses to finish the experiments differed among individuals (see RESULTS section).

Besides the major experiment described, we carried out an additional experiment to test the adequacy of the Embedded crab model. That is, we checked whether octopuses treated the Embedded crab (a Lifelike crab [a crab decoy] embedded in a transparent

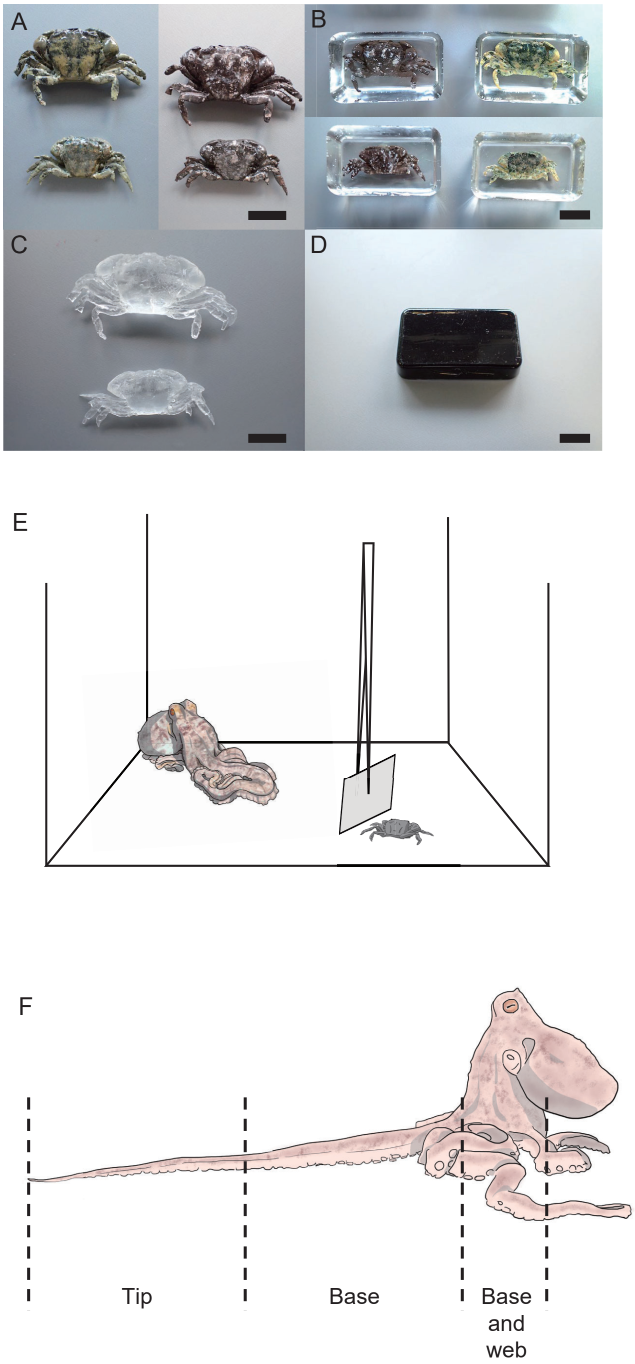

Fig. 1. Four models that were presented to plain-body octopus, *Callistoctopus aspilosomatis*, experimental procedure, and region of arm. **(A)** The Lifelike crab; similar to a crab in color and form. Green (left), black (right), large (upper), and small (lower). **(B)** The Embedded crab; similar to a crab in color and form but embedded in transparent cuboid. Green (left), black (right), large (upper), and small (lower). **(C)** The Translucent crab; similar to a crab in form but colorless. Large (upper) and small (lower). **(D)** The Black cuboid; a control. Black bars indicate 10 mm. **(E)** Using a pair of tweezers, a blindfold board (50 mm × 50 mm) with a model (the Lifelike crab, for example) behind it was put in an aquarium with an octopus. Then, the blindfold board was removed using a pair of tweezers, at which point the model was exposed to the octopus and the recording was started. **(F)** Octopus arm was divided into three regions, namely, tip (from the center to the tip), base (from the center to the base), and base and web (under the web).

cuboid) as a crab or as a crab in a transparent box. For this test, we presented two types of objects to octopuses: a jar with a white lid that contained a Lifelike crab (the crab decoy in the Embedded crab) (i.e., a crab in a transparent box), and a jar with a white lid without a Lifelike crab (i.e., a control) (Fig. 2). We used the same four models as in the experiment (two colors [green and black], and two sizes [large and small]) for models put in the jar. Both of these two jars contained coral gravel as a weight to cause submersion in water (Fig. 2). The jar that contained a Lifelike crab appeared as if the crab had been placed into a transparent tube. This appearance was more evident compared with that of the Embedded crab because the jar provided much more clear space around the crab decoy. In addition, the white lid closing the jar gave a strong impression, causing the jar to be obvious. If octopuses treated the Embedded crab as a transparent box with a crab inside, then the responses by octopuses to the Embedded crab and to the jar with a Lifelike crab would be similar. We recorded the rates of contact (percentage of trials in which the octopus contacted the model out of 20 trials) and the total time of contact (sum of the duration spent by the octopus in contact with a model within a single presentation) of four individuals (octopus A, C, E, and F) that had already participated in the major experiment of this study.

The behaviors of the octopuses were recorded with a digital video camera (Panasonic HC-VX992MT, Osaka, Japan) placed 0.5 m above the aquaria.

Analysis

We defined “contact with a model” as octopus touching or grasping a model by their sucker(s) and arm(s). Based on the amount of contact with the model, we calculated the rates of contact for each type of model. When an octopus contacted a model, we measured the following four variables: “total time of contact”, “latency”, “frequency of contact”, and “duration of contact”. The total time of contact is the sum of the duration spent by an octopus in contact with a model within a single presentation. The latency is the time from the point at which the experimenter presented the model to an octopus, to the point at which the octopus contacted the model. In many cases, an octopus repeated the contact with the model within a single presentation. The frequency of contact is the number of times of contact by an octopus within a single presentation, and the duration of contact is the average duration of a single contact (i.e., the total time of contact divided by the frequency of contact). We applied Friedman’s tests with Steel-Dwass’ tests in order to determine whether there were statistically significant differences among all combinations of results for each parameter measured in response to each model. Furthermore, to evaluate the change of the reaction of octopuses to each model as experiments progressed, we compared the two components of the total time of contact with each object—namely, the first five trials (the Lifelike crab-B [beginning], the Embedded crab-B [beginning], the Translucent crab-B [beginning], the Black cuboid-B [beginning]) and the last five trials (the Lifelike crab-E [end], the Embedded crab-E [end], the Translucent crab-E [end], the Black cuboid-E [end]). Subsequently, we applied the Wilcoxon signed-rank test in order to determine whether there were statistically significant differences between the beginning and the end of trials for presentation of each model.

For physical analysis, we recorded the region of octopuses’ arm(s) that contacted the model. We categorized the contacting behavior into the following three types according to the region of octopuses’ arm(s) that contacted the model: tip of arm(s) (region from the center to the tip), base of arm(s) (region from the center to the base) and base of arms and web (region around the mouth) (Fig. 1F). We recorded the time spent by octopuses in each behavioral category, and calculated the ratio of time spent in each category to the total time of contact with each model.

Fig. 2. Procedures that were used for additional experiments to investigate validity of the Embedded crab (a crab decoy embedded in a transparent cuboid). A jar containing the Lifelike crab (a decoy similar to a crab in color and form) **(A)**, and a jar without the Lifelike crab **(B)**. Both of these jars contained coral gravel as a weight to submerge the jar in water. These jars were presented to a plain-body octopus, *Callistoctopus aspilosomatis*, and its reactions were recorded. Black bars indicate 10 mm.

Ethics approval

Although ethics permission is not required for use of coleoid cephalopods in experiments in Japan, we treated our experimental animals according to the ethical rules for cephalopods adopted by European Union countries (Smith et al., 2013). For example, we reduced stress in our animals by covering the wall of each aquarium with a black cloth and by placing coral gravel on the entire bottom of the aquarium. Water conditions were always kept near natural levels, and water was aerated, even during transportation. When we conducted the autopsy, the octopuses were placed in seawater with 10% ethanol for euthanasia. We did not use negative reinforcement in the experiments.

RESULTS

Response of octopuses to a crab

The rate of contact by octopuses to a crab was 100% (Table 2). This was obvious because we selected the occasions when octopuses showed interest and contacted a crab, which we further proceeded to analyze for the model presentation experiments based on the prospect of continuous feeding motivation in octopuses (Table 2). When octopuses contacted the crab, they always ate it (see Supplementary Movie S1). Because octopuses took time to consume the crab, contact time with the crab became longer than contact time with any of the four models. In most of the cases, octopuses ate the crab in the first contact (Table 2, the frequency of contact was nearly 1.0).

Reactivity to the models

Octopuses actively responded to the four models in the

Table 2. Summary of reactions by plain-body octopuses *Callistoctopus aspilosomatis* that were presented a crab. Only octopuses that reacted to a crab were described.

		Average	Standard error	The first quartile	The second quartile	The third quartile
Rate of contact (%)*1		100	0	–	–	–
Latency (s)*2		–	–	16.25	52	156
Total time of contact (s)*3		–	–	4852.5	6124	7166.75
Frequency of contact*4		1.01	0.01	–	–	–
Duration of single contact (s)		–	–	4836	611.5	7164.5
Rate of contact region	Tip of arm(s) (%)	0.05	7.29E–05	–	–	–
	Base of arm(s) (%)	0.01	5.73E–05	–	–	–
	Base and web (%)	99.94	0.0001	–	–	–

*1 Rate of contact, the percentage of trials in which the octopus contacted the model out of 20 trials. *2 Latency, the time from the point at which the experimenter presented the model to an octopus, to the point at which the octopus contacted the model. *3 Total time of contact, the sum of duration spent by octopus to contact a model within a single presentation. *4 The frequency of contact, the number of times of contact by octopus within a single presentation.

order of the Lifelike crab, the Embedded crab, the Translucent crab, and the Black cuboid (Fig. 3A, the rate of contact ± SE, the Lifelike crab: 97.50 ± 1.71; the Embedded crab: 95.00 ± 3.16; the Translucent crab: 84.17 ± 3.00; the Black cuboid: 53.33 ± 4.59; see Supplementary Movies S2 S3, S4, S5). The rates of contact with the three types of models of crab (the Lifelike crab, the Embedded crab, and the Translucent crab) were significantly higher than that with the Black cuboid (Fig. 3A; Steel-Dwass' test, the Lifelike crab vs. the Black cuboid: $P = 0.017$, $t = 2.945$; the Embedded crab vs. the Black cuboid: $P = 0.018$, $t = 2.918$; the Translucent crab vs. the Black cuboid: $P = 0.020$, $t = 2.900$; $n = 6$) and the rate of contact of the Lifelike crab was also significantly higher than that of the Translucent crab (Fig. 3A; Steel-Dwass' test, $P = 0.043$, $t = 2.622$, $n = 6$). There was no significant difference in the rate of contact between the Lifelike crab and the Embedded crab (Fig. 3A; Steel-Dwass' test, $P = 0.949$, $t = 0.540$, $n = 6$). These tendencies for the rate of contact being the highest with the Lifelike crab and the Embedded crab and the lowest with the Black cuboid were present for each octopus individual.

All octopuses began to contact the three types of models of crab faster than they contacted the Black cuboid (Fig. 3B, median of the latency, the Lifelike crab: 32.00 s; the Embedded crab: 26.50 s; the Translucent crab: 65.00 s; the Black cuboid: 132.00 s). Furthermore, octopuses advanced significantly faster toward the Lifelike crab and the Embedded crab than toward the Black cuboid (Fig. 3B; Steel-Dwass' test, the Lifelike crab vs. the Black cuboid: $P = 0.0003$, $t = 4.155$; the Embedded crab vs. the Black cuboid: $P = 0.00002$, $t = 4.705$; $n = 6$). A similar trend was seen for the Translucent crab although the trend was not statistically significant (Fig. 3B). Among the three types of models of crab, the median of the latency was higher for the Translucent crab than for the other two models (Fig. 3B). This trend was common to four out of six individuals (octopus A, B, E, and F).

The rate of contact for the jar containing a Lifelike crab was higher than that of the jar without a Lifelike crab (the rate of contact ± SE, the jar that contained a Lifelike crab, 72.50 ± 7.15; the jar without a Lifelike crab, 56.25 ± 8.00) but less than that of the Translucent crab. The rate of the jar without a Lifelike crab was similar to that of the Black cuboid.

The total time of contact

The total time of contact in each model was high in the order corresponding to the Lifelike crab, the Embedded crab, the Translucent crab, and the Black cuboid (Fig. 3C, median of the total time of contact, the Lifelike crab: 99.00 s; the Embedded crab: 67.50 s; the Translucent crab: 42.00 s; the Black cuboid: 25.50 s). The medians of the total time of contact with the three types of models of crab (the Lifelike crab, the Embedded crab and the Translucent crab) were significantly higher than that with the Black cuboid (Fig. 3C; Steel-Dwass' test, the Lifelike crab vs. the Black cuboid: $P = 8.20\text{e-}12$, $t = 7.08$; the Embedded crab vs. the Black cuboid: $P = 1.16\text{e-}08$, $t = 6.00$; the Translucent crab vs. the Black cuboid: $P = 0.012$, $t = 3.06$; $n = 6$). Among the three types of models of crab, the medians of the total time of contact with the Lifelike crab and the Embedded crab were significantly higher than that with the Translucent crab (Fig. 3C; Steel-Dwass' test, the Lifelike crab vs. the Translucent crab: $P = 3.97\text{e-}05$, $t = 4.50$; the Embedded crab vs. the Translucent crab: $P = 0.\ 014$, $t = 3.003$; $n = 6$). Between the Lifelike crab and the Embedded crab, the median of the former was higher than that of the latter, although not with statistical significance (Steel-Dwass' test, $P = 0.367$, $n = 6$). The medians of the total time of contact in five out of six individuals (octopuses A–C, E, F) for the three types of models of crab were longer than that for the Black cuboid except for octopus D, in which the value for the Translucent crab (32.00 s) was slightly shorter than that for the Black cuboid (37.00 s). Among the three types of models of crab, five out of six individuals (octopus A, C–F) showed the longest value for the Lifelike crab except for octopus B, in which the value for the Embedded crab (133.5 s) was longer than that for the Lifelike crab (102.0 s). Also, five out of six individuals (octopus A–E) showed longer latency for the Embedded crab than the Translucent crab except for octopus F, in which latency for the Translucent crab (80.5 s) was longer than that for the Embedded crab (63.00 s).

We compared the total time of contact between the beginning and end of the trials for each of the four types of models. For all models, there was no significant difference between these two measurements, which indicated that the total time of contact did not change within a single model as the experiment progressed (Fig. 3D; Wilcoxon signed-rank

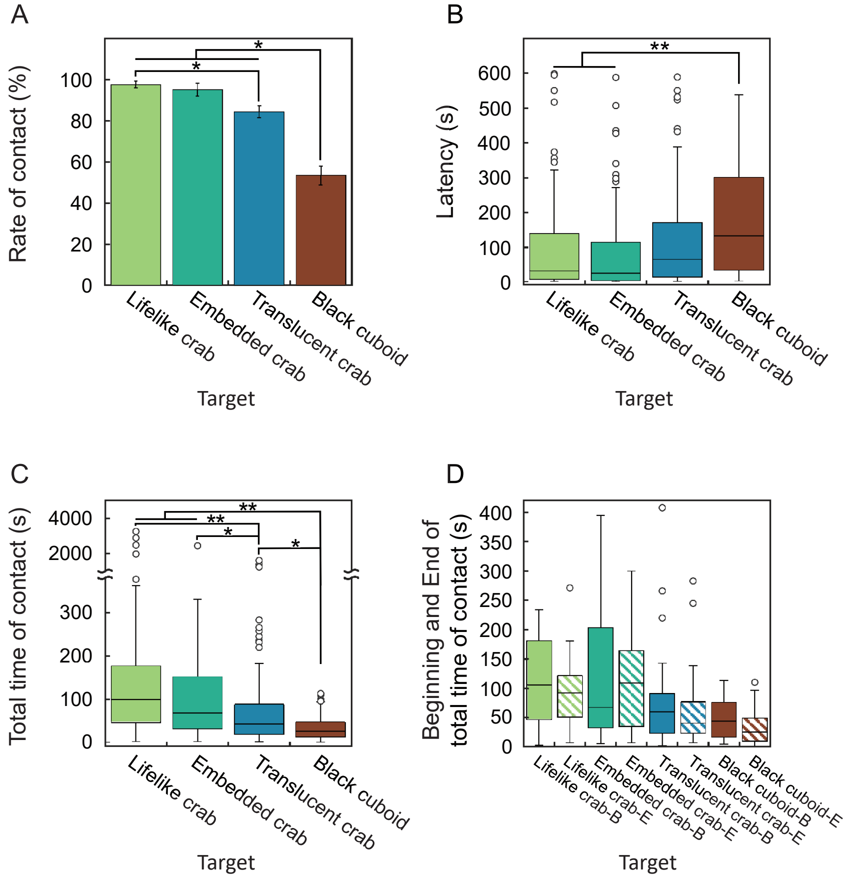

Fig. 3. The rate of contact, the latency, the total time of contact, and the trend of total time of contact over repeated trials by plain-body octopus, *Callistoctopus aspilosomatis*, for four types of models. We presented each model 20 times to six octopuses: **(A)** Mean rates of contact for the Lifelike crab (similar to a crab in color and form), the Embedded crab (similar to a crab in color and form but embedded in a transparent cuboid), the Translucent crab (similar to a crab in form but colorless), and the Black cuboid (a control). Bars represent standard error (Steel-Dwass' test, $*P < 0.05$). **(B)** The latency (the time from the point at which the experimenter presented the model to an octopus, to the point at which the octopus contacted the model) of octopuses for the four types of models. Central line indicates median, boxes represent 2nd and 3rd quartiles, and whiskers represent 1st and 4th quartiles. Dots denote outliers (Steel-Dwass' test, $**P < 0.01$). **(C)** The total time of contact (the sum of the duration spent by an octopus in contact with a model within a single presentation) by an octopus for the four types of models. Central line indicates median, boxes represent 2nd and 3rd quartiles, and whiskers the 1st and 4th quartiles. Dots denote outliers (Steel-Dwass' test, $*P < 0.05$, $**P < 0.01$). **(D)** The total time of contact of octopus for the first five trials (-B [beginning]) and the last five trials (-E [end]) for the four types of model. There was no significant difference between the beginning and the end of trials for each model (Wilcoxon signed-rank test, $P > 0.05$).

test, $P > 0.05$, n = six). For all models but the Embedded crab, the median time decreased at the end of the experiment (Fig. 3D). However, this trend was not shown by all individuals (number of individuals that showed a decreasing trend, the Lifelike crab: four [octopus B–E]; the Embedded crab: three [octopus A, C, E]; the Translucent crab: two [octopus B and E]; the Black cuboid: four [octopus A–C, F]).

The total time of contact for the jar containing a Lifelike crab was longer than that for the Black cuboid, but shorter than that for the Translucent crab (median [s], 33.22). The total time of contact for the jar without a Lifelike crab was shorter than that for the Black cuboid (median [s], 9.50).

Frequency and duration of contact

Octopuses more frequently contacted the three types of models of crab than the Black cuboid (Fig. 4A, the frequency of contact ± SE, the Lifelike crab: 4.55 ± 0.26; the Embedded crab: 4.40 ± 0.29; the Translucent crab: 3.50 ± 0.24; the Black cuboid: 2.06 ± 0.15). Frequencies of contact of the three types of models of crab were significantly higher than that of the Black cuboid (Steel-Dwass' test, the Lifelike crab vs. the Black cuboid: P = 6.40e-12, t = 7.12; the Embedded crab vs. the Black cuboid: P = 7.11e-10, t = 6.44; the Translucent crab vs. the Black cuboid: P = 1.43e-05, t = 4.72; n = 6). Also, the frequency of contact of the Lifelike crab was significantly higher than that of the Translucent crab (Fig. 4A; Steel-Dwass' test, P = 0.01, t = 3.09, n = 6). Although the Embedded crab was contacted more frequently than the Translucent crab, the difference was not statistically significant (Steel-Dwass' test, P = 0.64, n = 6). There was also no significant difference in contact frequency between the Lifelike crab and the Embedded crab (Steel-Dwass' test, P = 0.93, n = 6). All octopuses more frequently contacted the three types of models of crab than the Black cuboid, and they significantly more frequently contacted the Lifelike crab than the Black cuboid (Steel-Dwass' test, octopus A: P = 0.0001, t = 4.20; octopus B: P = 0.024, t = 2.84; octopus C: P = 0.047, t = 2.59; octopus D: P = 0.036, t = 2.69; octopus E: P = 0.003, t = 3.47; octopus F: P = 0.049, t = 2.58). Three out of six individuals significantly more frequently contacted the Embedded crab than the Black cuboid (Steel-Dwass' test, octopus A: P = 0.002, t = 3.64; octopus B: P = 0.0003, t = 4.02; octopus E: P = 0.002, t = 3.57), and two out of six individuals significantly more frequently contacted the Translucent crab than the Black cuboid (Steel-Dwass' test, octopus A: P = 0.019, t = 2.90; octopus E: P = 0.008, t = 3.19).

The durations of a single contact by octopuses with the Lifelike crab and the Embedded crab were significantly longer than those with the Translucent crab and the Black cuboid (Fig. 4B: medians of the duration, the Lifelike crab: 18.10 s; the Embedded crab: 18.81 s; the Embedded crab: 12.0 s; the Black cuboid: 12.67 s: Steel-Dwass' test, the Lifelike crab vs. the Black cuboid: P = 0.003, t = 3.45; the Embedded crab vs. the Black cuboid: P = 0.009, t = 3.14; the Lifelike crab vs. the Translucent crab: P = 0.007, t = 3.22; the Embedded crab vs. the Translucent crab: P = 0.04, t = 2.68; n = 6). Although the medians of the duration with the Lifelike crab and the Embedded crab were longer than

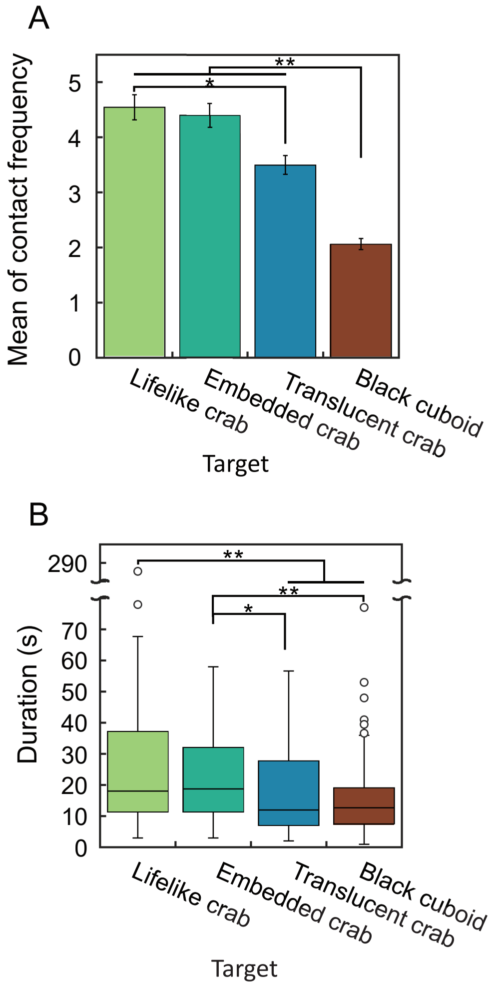

Fig. 4. **(A)** The mean frequency of contact in a single presentation (number of times of contact by octopus within a single task) of plain-body octopus *Callistoctopus aspilosomatis*. Bars represent standard error (Steel-Dwass' test, $^{*}P < 0.05$, $^{**}P < 0.01$). We presented each model 20 times to six octopuses. **(B)** The duration of single contact (average duration of single contact). Central line indicates median, boxes represent 2nd and 3rd quartiles, and whiskers 1st and 4th quartiles. Dots denote outliers (Steel-Dwass' test, $^{*}P < 0.05$, $^{**}P < 0.01$). We presented each model 20 times to six octopuses.

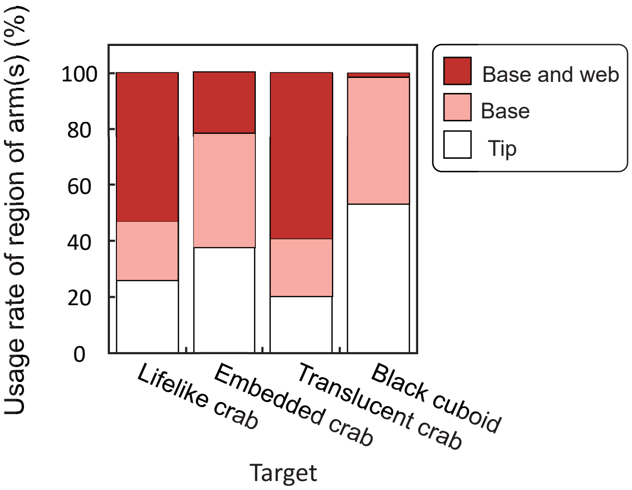

Fig. 5. The usage rate of regions of the arm of plain-body octopus, *Callistoctopus aspilosomatis*, when they contacted four types of models (the Lifelike crab [similar to a crab in color and form], the Embedded crab [similar to a crab in color and form but embedded in a transparent cuboid], the Translucent crab [similar to a crab in form but colorless], and the Black cuboid [a control]). We presented each model 20 times to six octopuses.

those with the Translucent crab and the Black cuboid for four out of six individuals (octopus A, C, D, and E), this trend was not statistically significant. The differences between the Lifelike crab and the Translucent crab in three octopuses (octopuses A–C) were that they contacted the Lifelike crab for a significantly longer period than the Translucent crab, and one octopus (octopus F) contacted the Translucent crab for a significantly longer period than the Black cuboid (Steel-Dwass' test, the Lifelike crab vs. the Translucent crab; octopus A: $P = 0.043$, $t = 2.63$; octopus B: $P = 0.043$, $t = 2.63$; octopus C: $P = 0.047$, $t = 2.59$; the Translucent crab vs. the Black cuboid; octopus F: $P = 0.019$, $t = 2.91$).

Usage rate of region of arm(s)

The composition of the usage rate of the region of arm(s) in each model could be divided into two types. Octopuses mostly contacted the Lifelike crab and the Translucent crab with the base of the arms and web (over 50% of total contact time), whereas octopuses contacted the Embedded crab and the Black cuboid the least with these regions (Fig. 5; the usage rate of the base of arms and web [%] ± SE, the Lifelike crab: 53.15 ± 0.13; the Embedded crab: 21.19 ± 0.12; the Translucent crab: 59.20 ± 0.11, the Black cuboid: 1.65 ± 0.01; see Supplementary Movies S2, S3, S4, S5). When octopuses contacted the Embedded crab and the Black cuboid, they used the tip of arm(s) or base of arm(s) almost equally (81.87–100% of total contact time) (Fig. 5; the usage rate of arm[s], the Embedded crab: the tip of arm[s]; 37.81 ± 0.07; the base of arm[s]; 40.79 ± 0.08; the Black cuboid: the tip of arm[s]; 53.18 ± 0.05; the base of arm[s]; 45.17 ± 0.05). These trends of the composition of usage rate of region of arm(s) were common in all individuals.

DISCUSSION

The importance of visual perception

The rates of contact in *C. aspilosomatis* were higher when the model being presented was visually similar to a crab. This was true even for the Translucent crab, which was different from a crab in color but identical in its contour. In cephalopods, for instance, squid *Todarodes pacificus* (Flores, 1983), cuttlefish *Sepia officinalis* (Messenger, 1968), and octopuses *O. vulgaris* (Maldonado, 1964) and *O. cyanea* (Forsythe and Hanlon, 1996) use visual cues for the primary phase of a sequential behavior for predation, which includes attention, positioning, and approach. A study on the sensory hierarchy between chemical and visual senses regarding food choice behavior showed that *O. vulgaris* chose preferred food from several options using a temporal hierarchy of primary visual sense and secondary chemical senses (Maselli et al., 2020). Our results indicate that *C. aspilosomatis* also use visual information of a target (i.e., appearance of a crab) for the primary phase of their hunting (i.e., attention and approach). Although movement of prey animals produces visual information, it is well documented that movement of prey animal is not necessary for predation by octopuses. For example, *O. vulgaris* hunted crabs which were stationary since their appendages had been removed (Wodinsky, 1971). This example also indicates that lack of movement of the models in this study would not influence the behavior of the octopuses.

On the other hand, octopuses exhibit a different type of hunting behavior in which they do not rely on visual information. For example, *O. cyanea* exhibit speculative hunting more frequently, in which they predominantly depend on tactile information (Yarnall, 1969). In this hunting tactic, octopuses spread the web over likely areas (e.g., a coral rock) where the prey hide, following which they receive tactile information of the prey that are in contact with the web and arms (Yarnall, 1969). Hunting behavior that depends on tactile information is also observed in other octopuses such as *O. vulgaris* (Mather and O'Dor, 1991), *Octopus briareus*, *O. bimaculatus*, *Octopus dofleini* (Hanlon and Messenger, 1996), and *Abdopus aculeatus* (Huffard, 2007). In this study, the place from which experimenter removed the blindfold board could have simulated a likely area of a prey for octopuses. If *C. aspilosomatis* predominantly apply a tactic to detect invisible prey, they would approach the likely area where the blindfold board was placed regardless of the types of models behind. However, although our octopuses paid attention by directing themselves to the blindfold board (i.e., they watched this board), they never approached it. Instead, they aggressively approached toward the models after the blindfold board was removed. This fact indicates that our octopuses depended on visual information of the target prey (the models of crabs in this case) rather than its tactile information in the primary phase of hunting.

Laboratory experiments examining visual responses to crabs by *O. vulgaris* (Young, 1956) showed that the probability of attacks on crabs by octopuses quickly rises if they are allowed to attack. In our current study, octopuses that definitely attacked the crab models mostly attacked the Lifelike crab and the Embedded crab. It is likely that the factors that make the probability of attack high are visual information of prey (a crab) and its tactile feedback. However, tactile feedback can work even if it lacks some amount of information of a crab, because the rate of contact of the Embedded crab was as high as the rate of the Lifelike crab. Also, this process is not strengthened by a reward (i.e., a prey) because octopuses could not eat the models finally.

It was also shown for *O. vulgaris* that latency to attack a crab was short (Young, 1956). In our current study, the latencies to contact the crab and the three types of models of crab were shorter than the latency to contact the Black cuboid. Furthermore, the latency of contact with the Translucent crab (colorless) being the longest among the three models of crab indicated that the octopuses also used visual stimulus for the primary phase of hunting.

In our previous study, *C. aspilosomatis* needed both visual and tactile information when they learned a novel object, in which they exhibited consecutive behavior such as touching after viewing a specific shape (Kawashima et al., 2021). Contrasting with this, in our current study, octopuses did not show such behavior with a novel object (i.e., three models of crab) being presented. This was likely because they already had their own image for a crab. Therefore, they merely matched the visual information of the model to the known visual information of a crab for judgement of primary hunting. In this context, the Lifelike crab and the Embedded crab fall in the category of potential prey for octopuses according to the past visuo-tactile experience in nature. It is of course a safe strategy for octopuses to primarily judge the potential prey by vision, in which they maintain distance from the target, rather than by touching it, which can expose them directly to a potential risk from the target.

Process of multisensory recognition

Because the total time of contact with a crab was much longer than that with the four models (see Table 2), we considered that the octopuses recognized the model as a crab when the total time of contact was longer. Among the four types of models, the total time of contact was the highest with the Lifelike crab. This indicates that octopuses use both visual and tactile information to further judge their potential prey. It is well known that octopuses possess good vison and tactility (Wells, 1978), by which they might be able to integrate these two senses to perceive their world. Interaction between visual and tactile sensory information in octopuses was previously suggested by a few earlier studies. For example, *O. vulgaris* that had learned to discriminate asperity (smooth as negative, and indented as positive) in translucent balls was able to be trained to perceive a smooth and colored ball as negative; subsequently, octopuses responded less to a rough and colored ball despite the fact that they had been trained to perceive it (but colorless) as positive (Allen et al., 1986). A similar phenomenon was also reported for *O. digueti* that had learned to perceive a smooth and colored ball as being positive, while a rough and transparent ball as being negative. If these octopuses subsequently experienced a different condition such as a rough and colored ball as being negative, they responded less to a smooth and colored ball (Michels et al., 1987). On the other hand, in a similar experimental context, *O. bimaculatus* and *O. vulgaris* (one individual was tested for each species) responded to an object, even though it contained a factor (color or texture) that had worked as being negative in the previous trial (Michels et al., 1987). Based on these findings so far obtained for octopuses, it is likely that memories formed by tactile experiences in octopuses strongly affect other memories formed by visual experiences, but variation exists for this phenomenon among species. Our previous studies of prickly octopus (Kawashima et al., 2020) and plain-body octopus (Kawashima et al., 2021) also indicated a similar possibility of visuo-tactile integration that had been suggested for *O. digueti* (Michels et al., 1987) and *O. vulgaris* (Allen et al., 1986), although the results with the latter species were not convincing (Michels et al., 1987). Actually, *A. aculeatus* learned more easily to touch a specific object under the condition that they could see and touch the object compared to the situation in which they could only see the object (Kawashima et al., 2020). Sensory integration of octopuses is also likely due to the fact that multisensory inputs are integrated in the brain areas involving learning and memory of *O. vulgaris* (Bertapelle et al., 2017). If octopuses are able to integrate visual and tactile information, it can be speculated that they access representations for a specific target from either visual or tactile stimulation that the target produces. During a benthic mode of life, octopuses are continuously exposed to various visual stimuli such as rocks, corals, sand, and live organisms, which are sometimes masked by turbid water or low light intensity. When the visibility is low, sensory integration processing derived from tactile stimulation must be useful. Furthermore, sensory integration derived from vision and touch must be adaptively accomplished in octopuses because of their body plan; they can touch the bottom with their arms and suckers equipped with tactile receptors, while they can look around with their eyes on the head that is positioned above their arms (Wells, 1978). On the other hand, although multisensory integration provides many advantages (e.g., improvement of detection, localization, orientation, and response speed; Stevenson et al., 2014), the integration of confliction from multiple senses could also lead to a decrease of perceptual reliability (Schumacher et al., 2016). To succeed in multisensory integration, animals need to estimate the reliability of each modality and use these estimates to weigh each signal appropriately when they are exposed to multisensory stimuli (Sheppard, 2013). This "weighing" of sensory inputs is known among vertebrates such as humans (visual and tactile: Violentyev et al., 2005; visual and auditory: Shams et al., 2002), rats (visual and auditory; Sheppard, 2013), and elephant nose fish *Gnathonemus petersii* (visual and electric; Schumacher et al., 2016). In the case of elephant nose fish, for example, they perceive electric information beyond visual information from their surroundings (Schumacher et al., 2016). Furthermore, these estimates of sense reliability are known to change flexibly depending on the situation and the subject to which the animals are exposed (Sheppard, 2013). In this study, when visual and tactile information of the models of crab were conflicted, octopuses seemed to use visual information as reliable information, which was shown by the fact that the total time of contact with the Embedded crab was significantly longer than that with the Translucent crab. This sense reliability, if it exists, can be seen in the variation of hunting tactics in octopuses among different habitats (*O. vulgaris*: Mather and O'Dor, 1991; *O. cyanea*: Forsythe and Hanlon, 1997; *Octopus insularis*: Leite et al., 2009). Although we currently examined sense reliability between vison and tactility for our octopuses only in a single situation (i.e., to capture the model), in the future, we plan to verify the dominant senses of octopuses for hunting under more situations with a combination of multisensory inputs from the target.

It is interesting that our octopuses dominantly used vison more than tactile information, even when they were allowed to contact the models that contained conflicting visual and tactile information, such as seen in the Embedded crab and the Translucent crab. This can be answered by the different perspective that the octopuses recognized the Embedded crab as a crab in a transparent box. In this speculation, there is no sensory conflict for octopuses, and they are willing to seize a crab in a box, as shown for *O. vulgaris* (Fiorito et al., 1990). To test this possibility, we conducted an additional experiment with a jar with a crab decoy (i.e., the Lifelike crab) present and absent and compared the results with the results for the models of a crab. If octopuses treated the Embedded crab as a transparent box with a crab inside, then responses by octopuses to the Embedded crab and the jar with a Lifelike crab must be similar. Our findings with this experiment indicated that the rate of contact and the total time of contact of the jar (with a crab decoy and corals) by *C. aspilosomatis* were greater than those of the Black cuboid, but they were less than those of the Translucent crab. The rate of contact and the total time of contact of a jar without a crab decoy were similar to those of the Black cuboid. These results indicate that our octopuses did not recognize the Embedded crab as a crab in a transparent box, and that they rather faced sensory conflict for tactile information.

Comparison between the total time of contact with the models at the start and end of the series of trials indicated that octopuses did not decrease reactivity to respond to the models in spite of the long period of trials that they attended. It is well known that octopuses have learning and problem-solving abilities such as visual discrimination of specific objects (Sutherland, 1962; Sutherland et al., 1963), tactile discrimination (Wells and Wells, 1957; Wells, 1964), observational learning (Fiorito and Scotto, 1992), maze learning (Moriyama and Gunji, 1997), and opening a jar with a plastic plug (Fiorito et al., 1990). *Callistoctopus aspilosomatis* that we currently studied is also able to learn an operant task in the laboratory (Kawashima et al., 2021). In addition, it is known that in octopuses, repeated trials without any rewards after the establishment of operant conditioning quickly induce extinction of learning and reduce responsiveness (Dews, 1959). If our octopuses learned through the relatively long period of the experiment that the presented models were inedible, the reactivity would be reduced, which was not the case, as mentioned above. Therefore, our octopuses reacted to each model and freshly received sensory information without learning its state as the experiment progressed.

Visual presentation of a crab decoy (i.e., the Lifelike crab or the Embedded crab) caused octopuses to pay attention to the decoy repeatedly during a single trial even after they scrutinized it visually and tactilely. It is well known that a series of stereotypical behaviors of animals for predation is induced by specific factors, which might be genetically programmed (Manning and Dawkins, 2012). This is also the case in cephalopods. For example, appearance of a prey (shrimp) and its specific movement (escaping to a vertical angle of 45°) can induce stereotypic hunting behavior of pharaoh cuttlefish, *Sepia pharaonis* (Shinzato et al., 2018). If the same process occurs in octopuses, it is likely that a crab decoy of the Lifelike crab or the Embedded crab would provide a visual stimulus for *C. aspilosomatis* and induce behavior such as attention and approach (i.e., the first phase of hunting). This is also supported by the fact that octopuses contacted the Translucent crab (colorless but with crab's contour) more often than the Black cuboid, and they contacted the former longer than the latter.

It is also notable that *C. aspilosomatis* contacted models that contain visual information of a crab for a long duration within a single occasion of contact (i.e., begin to contact — cease to contact). In humans, who can integrate multisensory information, one dominant sense affects sensory information from another sensory input. For example, when participants were exposed to one flash (visual information) and multiple beeps (auditory information) simultaneously, they perceived multiple flashes (Shams et al., 2002). Furthermore, when participants were exposed to one flash (visual information) and multiple taps of a finger (tactile information) simultaneously, they perceived multiple flashes (Violentyev et al., 2005). If we apply this sense effect phenomenon to our octopuses, it would explain their behavior as follows. When octopuses saw the Embedded crab, they received visual information of a crab decoy, and this visual input would produce a tactile illusion (i.e., touch of a crab) in octopuses while touching. Similarly, when octopuses saw the Translucent crab, they received visual information that was different from a crab, and a tactile illusion that accelerated a pseudo-tactile sense of octopuses on the Translucent crab. This may have made the octopuses perceive that the model was something different from a crab even though the tactility was similar to that of a crab. Further investigation is necessary to examine this possibility.

In cephalopods, brain regions that are intimately involved in tactile sensory processing are larger and more complex in octopuses than in squids and cuttlefishes (Nixon and Young, 2003). Furthermore, suckers of arms that work as tactile receptors are morphologically different between octopuses and squids or cuttlefishes, as the opening of the suckers of the latter two cephalopods is facilitated by chitinous denticulate rings, while octopuses lack this procedure (Hanlon and Messenger, 1996). These anatomical differences might produce different tactile sensory processing and variation of reliability of sensory integration among cephalopods (e.g., the lateral line analogue [Budelmann and Bleckmann, 1988], the epidermal lines [Bleckmann et al., 1991], and the olfactory organs [Gilly and Lucero, 1992] in squids and cuttlefishes). Future studies comparing hunting behavior among cephalopods would provide interesting insights into multisensory integration.

Physical function of tactile information

The usage rates of the region of arm(s) for contact among the four types of models indicated different tendencies compared to what was obtained from other measurements described. When octopuses contacted the Lifelike crab and the Translucent crab (similar tactile input of a crab), they dominantly used their base and web (over 50% of the total time of contact) as they did while feeding on a crab (99.94% of the total time of contact). As mentioned above, *C. aspilosimatis* seemed to rely on visual information of the model in the case of conflicting visual and tactile information (i.e., the Embedded crab and the Translucent crab). However, when octopuses held the Translucent crab model, they moved it toward their mouth while they received tactile information. When *O. vulgaris* extend their arms toward a target, or, when they grasp a food item and transfer it to their mouth via base and web, the octopuses exhibit stereotypic movement of arms (Sumbre et al., 2001). It is also known that the motor program for this stereotypic arm movement is embedded within the neural circuitry of the arm, since it has been shown that the arm of a normal octopus, as well as the arm of a decerebrated octopus, exhibited extension in the same manner (Sumbre et al., 2001). These facts tentatively suggest that tactile information from the Lifelike crab and the Translucent crab (i.e., tactilely similar to a crab) elicited arm movement of *C. aspilosomatis* while they held the models. However, octopuses integrated the model's tactile information with visual information, and they finally rejected the Translucent crab as a result of judgement based on visual information (i.e., translucent). This caused the total time of contact and the duration of contact with the Translucent crab to become shorter than those with Lifelike crabs that contain visual information of crab. On the other hand, the Embedded crab did not elicit octopuses' arm movement at an early phase because it lacked tactile information of a crab. Consequently, octopuses integrated tactile and visual information of the Embedded crab, during which they depended on visual information of this model (i.e., a crab decoy). Due to this processing, octopuses recognized the Embedded crab as a prey, and the total time of contact and the duration of contacts of this model became longer than those of the Translucent crabs.

In conclusion, this study clearly indicates that the octopus prioritizes visual and tactile information to detect prey. We examined it with unique unevenly formed models that represented their potential prey. In the primary phase of judgement, octopuses depend on visual information, and then they access the object tactilely, by which they process visuo-tactile integration. In case conflict arises between visual information and tactile information of the object, octopuses rely on the visual information for judgement. These findings can lead to the addition of octopuses to the list of animals with multisensory integration, and can also provide interesting comparisons for clarifying the evolutionary route of this advanced recognition ability among animals.

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COMPETING INTERESTS

The authors have no competing interest to declare.

AUTHOR CONTRIBUTIONS

SK and YI conceived and designed the study; SK performed the experiments and data analysis; SK and YI discussed the analyses and wrote the manuscript. YI supervised throughout the study.

SUPPLEMENTARY MATERIALS

Supplementary materials for this article are available online. (URL: https://doi.org/10.2108/zs210037)

Supplementary Movie S1. Plain-body octopus *Callistoctopus aspilosomatis* that is presented a crab.

Supplementary Movie S2. Plain-body octopus *Callistoctopus aspilosomatis* that is presented the Lifelike crab.

Supplementary Movie S3. Plain-body octopus *Callistoctopus aspilosomatis* that is presented the Embedded crab.

Supplementary Movie S4. Plain-body octopus *Callistoctopus aspilosomatis* that is presented the Translucent crab.

Supplementary Movie S5. Plain-body octopus *Callistoctopus aspilosomatis* that is presented the Black cuboid.

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