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The effects of visual impediment on the approaching behavior of harbor porpoise, *Phocoena phocoena*

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Abstract. Studies on odontocetes (e.g., porpoises) have revealed that these animals may adaptively use vision. The present study examined the contributions of vision to the approaching behavior of the harbor porpoise (*Phocoena phocoena*). When a porpoise approached a target, the time-to-contact perceived by the animal and its trajectory with a visual impediment condition were compared with those in the control (no impediment) condition. The results suggested that approaching behavior to a stationary target was guided by the animal's evaluation of time-to-contact (τ), maintaining the time derivative of τ ($\dot{\tau}$) at a constant value. A porpoise with visual deprivation exhibited greater $\dot{\tau}$ value and a longer evaluation time before contact than a porpoise that was not blindfolded in the task of reaching for the target. Furthermore, the porpoise with a visual impediment changed its swimming trajectory toward a target less than the control, which appeared to adaptively adjust its approaching trajectory. These findings imply that the use of vision aided echolocation and enables precise control and alteration of the trajectory during the approach. The present study has implications for adaptive use of vision during approaching behavior in the harbor porpoise.

Key words: locomotion, swimming trajectory, time-to-contact, visual deprivation, visual guidance.

Echolocation is a biological sonar system observed in a variety of animals, such as odontocetes and bats. These animals use self-generated sounds (clicks) and receive returning echoes from objects in their surroundings. In this study, we examined the effect of vision on an approaching behavior of odontocetes. Given that studies on odontocetes (e.g., porpoises) have documented that they rely on echolocation (Møhl and Andersen 1973; Au et al. 1999) to detect objects and enhance spatial awareness, we first review studies on echolocation in odontocetes, before describing the primary focus of this study.

In odontocetes, echolocation plays a major role in aquatic life, aiding in prey detection (Au and Snyder 1980; Au and Penner 1981; Kastelein et al. 1999; Moore et al. 2008), target discrimination (Au et al. 2009), and orientation (Norris et al. 1961; Verfuß et al. 2005). Porpoises exhibit specific echolocation activities during their

foraging behavior, adjusting the characteristics of the sound generated, such as the click interval, depending on situational demands (DeRuiter et al. 2009; Verfuß et al. 2009; Linnenschmidt et al. 2013). Thus, porpoises are widely acknowledged to use echolocation effectively.

One important issue is that porpoises may not emit clicks frequently enough to detect a target (Au and Jones 1991; Dawson 1991; Larsen et al. 2007). Therefore, regardless of the capabilities of the animals (e.g., Kastelein et al. 2000), they may fail to detect monofilament gillnets or may not perceive it as a threat, leading to entanglement and mortality as bycatch (Tregenza et al. 1997; Trippel et al. 1999; Hall et al. 2000; Natoli et al. 2008). Porpoises are known to emit clicks more frequently when entering new places or encountering unfamiliar objects (e.g., Akamatsu et al. 1994), and tend to emit fewer clicks toward habituated objects (Cox

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et al. 2001). Thus, porpoises appear to regulate their echolocation based on situational demands.

To date, several studies have focused on the involvement of vision in the acquisition of environmental information and have documented the anatomical structures and features of the eyes of porpoises. Porpoise eyes adapt to the poor visual conditions of the aquatic environment, where luminosity is low at greater depths and light is strongly scattered by suspended solids in the water (Mass and Supin 2007). Their structure differs from terrestrial mammalian eyes in the form of the lens and pupil and in the distribution of ganglion cells in the retina (e.g., Mass et al. 1986; Kröger and Kirschfeld 1993; Murayama et al. 1995). Porpoises benefit from these structures to obtain the best visual field in both forward and lateral directions, along with underwater acuity at near distances (Murayama et al. 1995) that is much better than that of some terrestrial animals (Murayama and Somiya 1998). Despite these findings, few studies have investigated the role of vision in spatial localization of porpoise. During approaching a target, obtaining visual information may enhance a porpoise's spatial awareness, thus allowing the porpoise to adaptively adjust its approaching trajectory and precisely control its reaching movement.

This study examined the involvement of vision in the approaching behavior toward a stationary target in the harbor porpoise (*Phocoena phocoena*). The vision of the porpoise was impeded in the experimental condition (visual impediment), and no such manipulation was implemented in the control condition. Compared with the control condition, we hypothesized that visual impairment would alter the porpoise's swimming trajectory, and that the porpoise would reduce its swimming speed to avoid hitting the target. We sought to assess the importance of vision during the approach phase, in which echolocation is considered to play the major role.

The ability to approach a target was assessed by the τ (tau) value, $\dot{\tau}$ (tau-dot) value, and the trajectory of the swimming track. The τ and $\dot{\tau}$ values were proposed in an early study (Lee 1976) to represent sensory information contributing to the control of approach speed and deceleration. Specifically, approaching behavior is guided by an animal's evaluation of the time-to-contact (τ), which is the time margin before contact with an object, and the time derivative of τ ($\dot{\tau}$).

The time-to-contact can be determined through visual cues (Lee 1976; Wagner 1982) and auditory cues (e.g., Lee et al. 1992, 1995; Lutfi and Wang 1999) by animals. Time-to-contact information perceived by animals (τ ; not

Table 1. Summary of implications of the tau-dot value regarding movement of animals during the approach, modified from Lee (1993)

Value of tau-dot ($\dot{\tau}$)	Implied movement of animal	Effect of keeping tau-dot constant
$\dot{\tau} > 1$	Accelerating	Contacts
$\dot{\tau} = 1$	Constant velocity	Contacts
$0.5 < \dot{\tau} < 1$	Decelerating	Controlled contact (braking increases)
$\dot{\tau} = 0.5$	Decelerating	Stops at (braking constant)
$0 < \dot{\tau} < 0.5$	Decelerating	Stops at (braking decreases)

If $0.5 < \text{tau-dot} < 1$, contact will ensue and a larger value of tau-dot means that the animal decelerated abruptly.

the actual time-to-contact) can be calculated using the common function: $\tau = x/\dot{x}$, where x is distance to an object and \dot{x} is approach speed. During the approach, animals control their speed toward a stationary object by maintaining $\dot{\tau}$ at a constant value (Lee et al. 1992, 1993). Therefore, τ decreases linearly with a decreasing time-to-contact value. More importantly, maintaining a constant $\dot{\tau}$ affects the movement of the animal during its approach to a target (Table 1; Lee et al. 1992). If the animal wants to stop at the target after its approach then deceleration must be controlled to prevent contact with, or stopping short of, the target. When $\dot{\tau}$ is 0.5, the animal will stop at the position of the target by maintaining constant deceleration. If $\dot{\tau}$ is larger than 0.5, the animal should increase its rate of deceleration during its approach to prevent contact with the target, and its speed at the end point will be higher (Lee et al. 2009). For a porpoise to catch a fish, it is not necessary to stop at the target location; thus, $\dot{\tau}$ should be $0.5 < \dot{\tau} < 1$, indicating that the porpoise is on a controlled contact course. However, if the porpoise precisely evaluates and predicts relative velocities and the position of the target during its approach, $\dot{\tau}$ will be maintained at around 0.5. If $\dot{\tau}$ is considerably less or greater than 0.5, the initial deceleration should be adjusted as necessary to stop at the target. Thus, if visual cues enhance a porpoise's spatial awareness during the approach to an object, it can precisely control its approach, maintaining $\dot{\tau}$ at a constant value of approximately 0.5.

Materials and methods

Animal

One male harbor porpoise was involved in the present study. The porpoise was incidentally captured by a

large set net in Usujiri, Hakodate, Hokkaido, Japan. The porpoise was acclimated in a pool at Usujiri Fisheries Station, Hokkaido University, and was transported to Otaru Aquarium for health management. The porpoise was SNH08008-2 (named Teppei by the Stranding Network Hokkaido and was incidentally caught on April 20, 2008). No serious health problems were identified in the animal.

Ethics statement

The experiments were conducted under approval of the National University Corporation Hokkaido University Animal Experimentation Committee permit 12-0004 in April 2014. This study was conducted under the supervision of a veterinarian at Otaru Aquarium, Hokkaido, Japan for health management of the animal.

Study site

The experiments were conducted in a $6.0 \times 3.7 \times 1.9$ m indoor concrete pool, which is an auxiliary water pool for medical treatment, so that the animal could acclimate to the indoor pool conditions for behavior experiments at Otaru Aquarium (Fig. 1). A scaffold for feeding was placed on one side of the short wall that was approximately 0.2 m from the water surface. The animal was unable to swim deeply, because the water level of the pool was kept at approximately 1.3 m during the experiments. The ambient light illuminance level was maintained at approximately 500 lux. The porpoise involved in the experiment was well acclimated to the study conditions. It should be noted that the experimental setting differed from the natural environment.

Experimental setup

A video camera (C920t, Logitech International S.A.) was placed 2.3 m above the scaffold in the pool for video recording. The camera mounted on the ceiling of the facility recorded a top view of a $2.0 \text{ m} \times 2.3 \text{ m}$ range in the pool (Fig. 1). The camera was directly connected via a universal serial bus extension cable to a computer that was placed at a remote location and monitoring the behavior of the animal.

We used dead fish, including mackerel (*Scombridae* sp.), Atka mackerel (*Pleurogrammus azonus*), and sand launces (*Ammodytes personatus*), as target objects. Their sizes were approximately 15–30 cm. These species comprise the standard diet of the animal in the aquarium and are easy to identify as targets for the animal to approach. The target objects were fed to the animal by directly

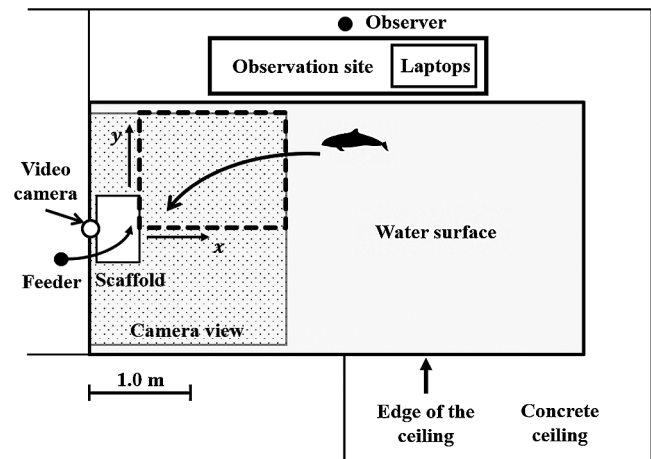


Fig. 1. Top view of the study area. The diagram shows the locations of the scaffold and the video-recording devices. The observation site was placed poolside to visually inspect the behavior of the animals. The video images yielded rectangular coordinates such that the longer and shorter side of the water surface represent the x- and y-coordinates, respectively.

suspending by hand from the scaffold, so that the fish was presented in the water without immersing the hands. The species of fish was chosen randomly on a trial by trial basis.

We used blindfolding to introduce a visual impediment. The eyes were masked by placing a pair of opaque silicone suction cups (Cetacean Research Technology) over the eyes for the visual impediment condition. These suction cups were attached to each eye before initiating the trials, and the animal's behavior was carefully monitored to avoid injuring the animal. Blindfolding was conducted underwater, with more than two experimenters holding the porpoise's body. No visual manipulation was used for the control condition.

Procedure

The experiments were conducted from October 6 to 12, 2014 for the porpoise (Appendix 1). Data for the porpoise were collected during two time periods per day, in the morning (7:00–9:00) under the visual impediment condition and at noon (12:00) under the control condition.

The animal was transported to the testing pool one day before the experiment, so that the animal habituated to the pool environment. We conducted a pre-test of the blindfolding procedure before initiating measurement to habituate the animal to the impediment condition. Furthermore, under the visual impediment condition, we allowed the animal to rest for 2–5 min after blindfolding.

At the beginning of each trial, one animal feeder climbed the scaffold to present the target, while the porpoise was positioned at the opposite side of the scaffold, more than 1.5 m away from the target. Each animal's behavior was recorded and monitored, until it successfully reached the target. The set of trials continued until the animal did not approach the object within five min.

Video data collection

Thirty video images per second were sampled using webcam software (Logicool webcam software version 2.51, Logitech International S.A.), and each frame was analyzed using video analysis software (Tracker version 4.86, Douglas Brown). The images were collected 8.1 seconds before the animal reached the target (1.5 m maximum approaching distance). These images were applied to a rectangular x or y-coordinate system, and the origin was defined as the target position. The tip of the rostrum of the animal was defined as the animal's position at time t in a swimming track. Because the coordinates included a position error when they were sampled manually, the values were corrected by calculating a simple moving average over three consecutive coordinate x or y values (Equation 1):

$$X'_t = \frac{X_{t-1} + X_t + X_{t+1}}{3} \quad (1)$$

where X' is the corrected coordinate x or y value, and X is the coordinate value. These corrected values were plotted as the coordinates of the trajectories of the porpoise.

The behavior of the porpoise was video-recorded when the rostrum was clearly visible. Incomplete trials, such as those in which the animal's rostrum was invisible, were discarded due to the lack of image clarity for accurately determining the coordinates. We obtained swimming track records from 84 trials, yielding 9548 video frames: these included 18 trials (2344 frames) under the visual impediment condition and 66 trials (7204 frames) under the control condition.

Time-to-contact perceived by the porpoise

From each video frame, we calculated the distance between the animal and the target, as well as the animal's speed. Then, we calculated τ as the ratio of the distance to the speed (Lee 1976), indicating the time-to-contact perceived by the animal (Equation 2):

$$\tau = \frac{Z_t}{V_t} \quad (2)$$

where Z_t is the distance to the target from the animal's rostrum at each frame of time t and V_t is the animal's speed.

We also investigated whether $\dot{\tau}$, the time derivative of τ , was constant during the approaching behavior. If the porpoise maintains $\dot{\tau}$ constant as $0.5 < \dot{\tau} < 1$ to control its speed, the plot of τ against the time-to-contact should be linear, and the deceleration rate should vary over time and eventually increase. Thus, we determined that $\dot{\tau}$ and the deceleration value were consistent when the R^2 value of the simple regression line was greater than 0.5. Equation 3 is the formula for the regression line in which τ depends on the time-to-contact.

$$\tau_t = \beta + \dot{\tau} \times t \quad (3)$$

where β is the intercept of the regression line. The slope of the regression line approximated the constant $\dot{\tau}$ value maintained by the porpoise, indicating whether the animal's braking was soft or hard during the experimental time window (~8.1 seconds). We assessed the consistency of the deceleration value in relation to the time-to-contact calculating by the R^2 value of the regression line, with $\dot{\tau}$ as the slope value (Equation 4):

$$V_t = \beta + \dot{v} \times t \quad (4)$$

Fluctuation of swimming trajectories

We assessed fluctuation of trajectories using two indices: the deviation of the position angles and the residuals from a linear regression line.

First, the position angle (θ) in radians ($-\pi < \theta < \pi$) indicates the argument of each position (x, y) in the coordinate system. A high variance of the position angle showed or indicated that the trajectory is highly distorted. Fluctuation occurred when the animal frequently moved its body or head direction with respect to the target. The position angles were obtained by dividing the y-coordinate by the x-coordinate value (Equation 5):

$$\theta = \tan^{-1} \frac{y}{x} \quad (5)$$

The second index employed was the residuals from the orthogonal regression line (e.g., Carroll and Ruppert 1996), which were fit to the trajectory. A high residual value predicted that the trajectory was highly distorted, indicating the trajectory deviated from a linear track. As the mean value of the residuals was zero, we calculated the absolute values of the residuals. Statistical analyses were performed in R 3.5.1 for Windows (R Development Core Team 2018).

Results

Approaching behavior of the animal

Figure 2 shows the plot of approaching speed against time-to-contact value. The mean and *SE* of the mean speed for each trial per experimental condition are shown in Table 2. The speed in the visual impediment condition was slower than that in the control condition (Wilcoxon rank sum test; $W = 217.5$, $P < 0.001$). To examine whether deceleration during approach varied over time, we applied a simple linear regression analysis to the individual plots (gray lines in Fig. 2). Not all of the regressions were statistically significant. Specifically, 5 of the 18 visual impediment trials (F -test, $P \leq 0.555$) and 6 of the 66 control condition trials (F -test, $P \leq 0.997$) were not significant. The mean (and *SE*) of the R^2 values across the regression lines were 0.30 (0.06) under the visual impediment condition, and 0.40 (0.04) under the control condition. Thus, deceleration did not

remain constant but varied over time.

For further testing, we applied deceleration against the time-to-contact to additive models with a smooth spline function (R version 3.5.1 mgcv package, Fig. 3). The optimum degree of smoothing was defined by the minimum generalized cross validation (GCV). The porpoise in the two conditions increased its deceleration approximately 2 seconds before contact with the target. However, the deceleration pattern differed between the two conditions. Under the visual impediment condition, the porpoise increased its approaching speed 2 seconds before the contact and eventually decreased the speed. Under the control condition, however, the porpoise once increased approaching speed approximately 7–8 seconds before the contact and eventually decreased its speed 2 seconds before contact. The speed when the porpoise contacted the target was greater under the visual impediment condition than under the control condition.

Figure 4 shows a plot of the τ with the time-to-contact

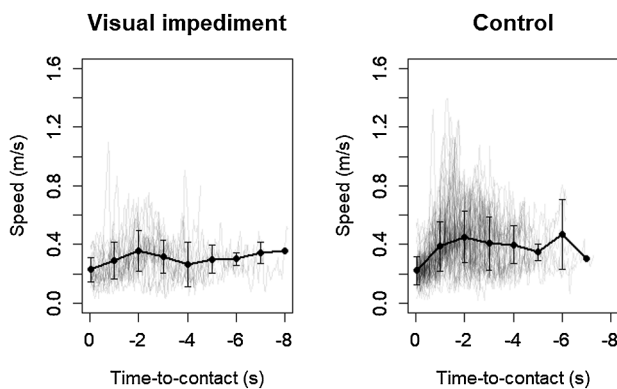


Fig. 2. The plot of mean and *SD* per second of the speed (ms^{-1}) for each trial as a function of time-to-contact (s) under the experimental conditions. The gray lines represent individual plots of the approaching velocities of each trial.

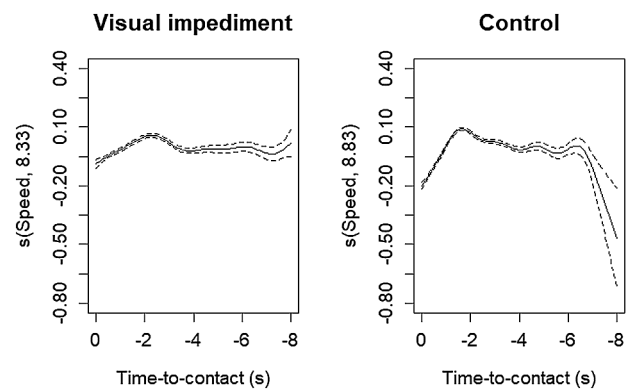


Fig. 3. Smoothed curves of the approaching speed (ms^{-1}) averaged over trials against time-to-contact (s). The estimated 95% confidence interval are shown by the dotted line with the smoothed curves. The number *df* in $s(\text{Speed}, df)$ is the number of degrees of freedom of the smooth spline.

Table 2. Means and *SE* of variables during approaching behavior obtained from the harbor porpoise under the experimental conditions

Variables	Visual impediment		Control		<i>W</i>
	Mean	<i>SE</i>	Mean	<i>SE</i>	
Speed (m/s)	0.314	0.004	0.416	0.001	217.5***
Tau (s)	-1.584	0.033	-1.253	0.009	383.0*
Tau-dot	0.705	0.010	0.616	0.003	791.5*
Position angle <i>SD</i> (rad)	0.133	0.004	0.215	0.001	265.0***
Residuals (m)	0.037	0.001	0.072	0.0005	180.0***

Note: W = Wilcoxon test statistic.

* $P < 0.05$, *** $P < 0.001$.

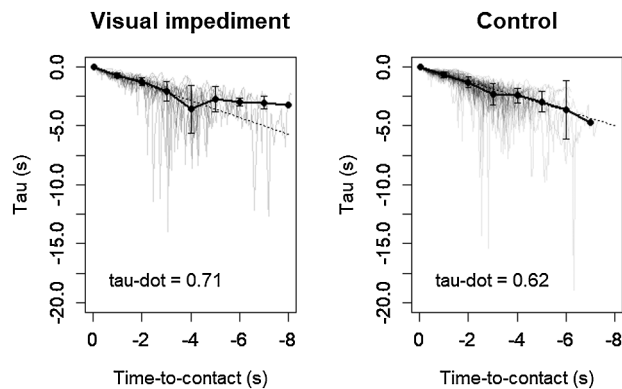


Fig. 4. The plot of mean and *SD* per second of the τ (s) for each trial as a function of time-to-contact (s) under the experimental conditions. The individual plot of the τ of each trial are shown by the gray lines. The slope of the regression line (dotted line) represents the constant $\dot{\tau}$ maintained by porpoise.

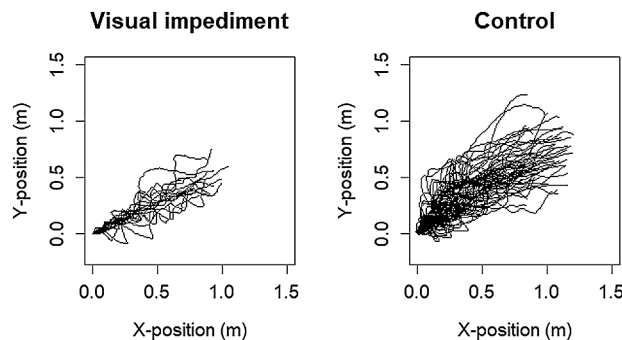


Fig. 5. Trajectory lines during the approaching behavior of the porpoise. The origin of the trajectories (0, 0) is the position where the target was displayed. The x- and y-coordinates are the longer and shorter sides of the pool, respectively.

values. To examine whether the porpoise decreased τ linearly over time, we applied a simple linear regression analysis to each individual plot (gray lines in Fig. 4). The results showed that all regression lines were significant: the mean and *SE* of the R^2 value over the regression lines was 0.68 (0.04) under the visual impediment condition (F -test, $P < 0.001$), and 0.74 (0.02) under the control condition (F -test, $P < 0.001$). The R^2 values were greater than those of lines for deceleration in the visual impediment condition ($t = 5.34$, $df = 32$, $P < 0.001$) and the control condition ($t = 8.17$, $df = 97$, $P < 0.001$).

Table 2 shows the mean and (*SE*) of the constant $\dot{\tau}$ value maintained by the animal, calculated from the regression line for each trial per experimental condition: the values were 0.71 (0.01) for the visual impediment condition and 0.62 (0.003) for the control condition. These values were greater than 0.5 ($t = 34.7$, $df = 108$,

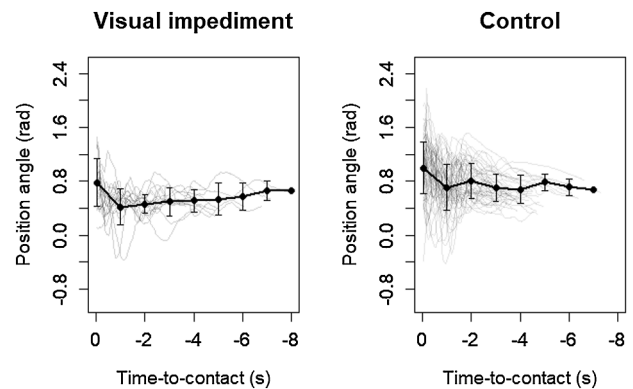


Fig. 6. The plot of mean and *SD* per second of the position angle (rad) for each trial as a function of time-to-contact (s) under the experimental conditions. The gray lines represent the individual transitions in each trial of the reference index that predicted fluctuation of the trajectory.

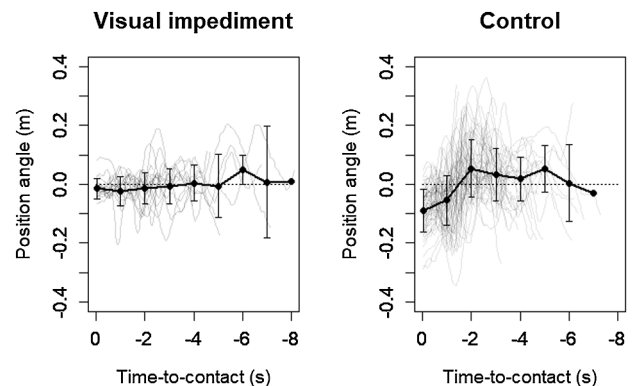


Fig. 7. The plot of mean and *SD* per second of the residual value (m) from the orthogonal regression line for each trial as a function of time-to-contact (s) under the experimental conditions. The gray lines represent the individual transitions in each trial of the reference index that predicted fluctuation of the trajectory. The dotted line with a residual value of 0 represents the normalized orthogonal regression line.

$P < 0.001$), and $\dot{\tau}$ under the visual impediment condition was larger than that in the control condition (Wilcoxon rank sum test; $W = 791.5$, $P = 0.031$).

Table 2 shows the mean and *SE* of the mean τ value for each trial per experimental condition. The values show that over the time series the porpoise perceived a greater time margin before contact under the visually impediment condition than under the control condition (Wilcoxon rank sum test; $W = 383$, $P = 0.021$).

Swimming trajectories

The trajectories of all trials are shown as solid lines in Fig. 5. The porpoise often swam in a counterclockwise direction, so that it approached from the first quadrant of

the coordinate system (dotted line in Fig. 1) with the target as the origin. Visual observation of the porpoise's behavior revealed that under the control condition it sometimes approached close to the fish and remained in that position instead of swimming away. From each position of the coordinates, the time-series change in the position angle was obtained (Fig. 6). The mean and *SE* of the mean standard deviation value of the position angles for each trial (Table 2) was significantly smaller for the visual impediment condition than for the control condition (Wilcoxon rank sum test; $W = 265$, $P < 0.001$). The residual distance from the orthogonal straight line to the target predicted fluctuation in the trajectory (Fig. 7), and the mean value was significantly smaller under the visual impediment condition (Table 2) than under the control conditions (Wilcoxon rank sum test; $W = 180$, $P < 0.001$).

Discussion

The present study examined the involvement of vision in the approaching behavior of a harbor porpoise using stationary targets. The following findings were obtained from the analysis. The τ value linearly decreased with decreasing time-to-contact, indicating the $\dot{\tau}$ was approximately constant, while deceleration varied over time and eventually increased. The constant $\dot{\tau}$ maintained by the porpoise was closer to 0.5 under the control condition than under the visual impediment condition, indicating that with no visual impediment the porpoise evaluated its approach speed and controlled its deceleration appropriately. Additionally, the blindfolded porpoise required a greater time margin before contact than without blindfolding. Focusing on the approach trajectories, fluctuations in the trajectories were greater without blindfolding than with blindfolding. Thus, we concluded that the use of vision aided echolocation sensing and enabled precise control and alteration of the trajectory during the approach.

Evaluating the time-to-contact reveals an animal's precise control of its behavior while reaching for the target (Lee et al. 1992). The present results suggest that the porpoise maintained a constant $\dot{\tau}$ to control its approach speed and deceleration behavior toward contact with the target. Specifically, under the control condition, the porpoise initially (7–8 seconds before contact) increased the speed and eventually (2 seconds before contact) decreased the speed to contact with the target. However, the porpoise under the visual impediment condition increased the speed approximately 2 seconds

before contact and then immediately decreased the speed. The porpoise was able to contact with the target at a lower speed under the control condition than the visual impediment condition, indicating that the porpoise without visual impediment decreased its speed to stop at the target, whereas the porpoise with visual impediment did not. With visual impediment, the porpoise could not measure the time before contact with the target precisely (i.e., large time margin before collision), causing that porpoise would immediately adjust its speed near the contact. Thus, we conclude that visual cues aided control of its contact with the target.

The lack of visual cues affected changes to the animal's trajectory approach. As mentioned in the results, we found that the porpoise sometimes approached close to the fish and remained in that position instead of swimming away in the control condition. A similar finding by Verfuß et al. (2009) revealed a difference in porpoise behavior with and without eyecups, such that porpoises without visual deprivation often turned their body to a belly-up position to catch fish. These findings suggested that the use of visual cues increased animal's maneuverability. In the experiment the porpoise with visual impediment would not be able to measure precise distance to the target just using echolocation, and thus the porpoise approached carefully without large fluctuation of trajectory and speed compared to the control condition. Thus, the use of visual cues may aid the porpoise's performance in approaching.

The influence of blindfolding during locomotion for porpoises has been documented previously (e.g., Wood and Evans 1980; Verfuß et al. 2009). For example, porpoises with eyecups had slower swimming speeds (approximately 5 ms^{-1}) than those (approximately 3 ms^{-1}) without eyecups (Verfuß et al. 2009). This finding is consistent with the present results, although the speeds recorded in the present study were much slower than those in the previous study. Blindfolded porpoises might compensate for the lack of vision by increasing the number of clicks emitted per meter (Verfuß et al. 2005). Thus, the lack of vision reduces information available, although echolocation plays a major role in driving porpoise behavior. We note that approaching behavior in the present study might have been affected by possible confounding factors such as the form and size of the tank, the animal's acclimation to the task, and its memory of the target location. To exclude these factors, further investigation is required to control for these experimental conditions.

To conclude, the sensory modalities for wild odontocetes have not been described well except for echolocation research. Specifically, some species of odontocetes may approach prey using passive sound cues, such as the swimming sounds of their prey (e.g., Barrett-Lennard et al. 1996). It is assumed that most species of odontocetes have good vision (Mass and Supin 2007), which they use for approaching and examining objects (e.g., Yaman et al. 2003). Fristrup and Harbison (2002) described that vision may play an important role in sperm whale predation. The findings of the present study contribute to understanding of the primary sensory modalities of wild odontocetes during approaching behavior. Measuring and comparing approaching behaviors with an auditory impediment would provide further insights into how odontocetes use multi-sensory information.

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References

- Akamatsu, T., Hatakeyama, Y., Kojima, T. and Soeda, H. 1994. Echolocation rates of two harbor porpoises (*Phocoena phocoena*). *Marine Mammal Science* 10: 401–411.
- Au, W. W. L., Branstetter, B. K., Benoit-Bird, K. J. and Kastelein, R. A. 2009. Acoustic basis for fish prey discrimination by echolocating dolphins and porpoises. *Journal of the Acoustical Society of America* 126: 460–467.
- Au, W. W. L. and Jones, L. 1991. Acoustic reflectivity of nets implications concerning incidental take of dolphins. *Marine Mammal Science* 7: 258–273.
- Au, W. W. L., Kastelein, R. A., Rippe, T. and Schooneman, N. M. 1999. Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). *Journal of the Acoustical Society of America* 106: 3699–3705.
- Au, W. W. L. and Penner, R. H. 1981. Target detection in noise by echolocating Atlantic bottlenose dolphins. *Journal of the Acoustical Society of America* 70: 687–693.
- Au, W. W. L. and Snyder, K. J. 1980. Long-range target detection in open waters by an echolocating Atlantic Bottlenose dolphin (*Tursiops truncatus*). *Journal of the Acoustical Society of America* 68: 1077–1084.
- Barrett-Lennard, L. G., Ford, J. K. B. and Heise, K. A. 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour* 51: 553–566.
- Carroll, R. J. and Ruppert, D. 1996. The use and misuse of orthogonal regression in linear errors-in-variables models. *American Statistician* 50: 1–6.
- Cox, T. M., Read, A. J., Solow, A. and Tregenza, N. 2001. Will harbour porpoises (*Phocoena phocoena*) habituate to pingers? *Journal of Cetacean Research and Management* 3: 81–86.
- Dawson, S. M. 1991. Modifying gillnets to reduce entanglement of cetaceans. *Marine Mammal Science* 7: 274–282.
- DeRuiter, S. L., Bahr, A., Blanchet, M.-A., Hansen, S. F., Kristensen, J. H., Madsen, P. T., Tyack, P. L. and Wahlberg, M. 2009. Acoustic behaviour of echolocating porpoises during prey capture. *Journal of Experimental Biology* 212: 3100–3107.
- Fristrup, K. M. and Harbison, G. R. 2002. How do sperm whales catch squids? *Marine Mammal Science* 18: 42–54.
- Hall, M. A., Alverson, D. L. and Metuzals, K. I. 2000. By-catch: problems and solutions. *Marine Pollution Bulletin* 41: 204–219.
- Kastelein, R. A., Au, W. W. L. and de Haan, D. 2000. Detection distances of bottom-set gillnets by harbour porpoises (*Phocoena phocoena*) and bottlenose dolphins (*Tursiops truncatus*). *Marine Environmental Research* 49: 359–375.
- Kastelein, R. A., Au, W. W. L., Rippe, H. T. and Schooneman, N. M. 1999. Target detection by an echolocating harbor porpoise (*Phocoena phocoena*). *Journal of the Acoustical Society of America* 105: 2493–2498.
- Kröger, R. H. H. and Kirschfeld, K. 1993. Optics of the harbor porpoise eye in water. *Journal of the Optical Society of America A* 10: 1481–1489.
- Larsen, F., Eigaard, O. R. and Tougaard, J. 2007. Reduction of harbour porpoise (*Phocoena phocoena*) bycatch by iron-oxide gillnets. *Fisheries Research* 85: 270–278.
- Lee, D. N. 1976. A theory of visual control of braking based on information about time-to-collision. *Perception* 5: 437–459.
- Lee, D. N., van der Weel, F. R., Hitchcock, T., Matejowsky, E. and Pettigrew, J. D. 1992. Common principle of guidance by echolocation and vision. *Journal of Comparative Physiology A* 171: 563–571.
- Lee, D. N., Davies, M. N. O., Green, P. R. and van der Weel, F. R. 1993. Visual control of velocity of approach by pigeons when landing. *Journal of Experimental Biology* 180: 85–104.
- Lee, D. N., Simmons, J. A., Saillant, P. A. and Bouffard, F. 1995. Steering by echolocation: a paradigm of ecological acoustics. *Journal of Comparative Physiology A* 176: 347–354.
- Lee, D. N., Bootsma, R. J., Land, M., Regan, D. and Gray, R. 2009. Lee's 1976 Paper. *Perception* 38: 837–858.
- Linnenschmidt, M., Teilmann, J., Akamatsu, T., Dietz, R. and Miller, L. A. 2013. Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena phocoena*). *Marine Mammal Science* 29: E77–E97.
- Lutfi, R. A. and Wang, W. 1999. Correlational analysis of acoustic cues for the discrimination of auditory motion. *Journal of the Acoustical Society of America* 106: 919–928.
- Mass, A. M. and Supin, A. Y. 2007. Adaptive features of aquatic mammals' eye. *The Anatomical Record* 290: 701–715.
- Mass, A. M., Supin, A. Y. and Severtsov, A. N. 1986. Topographic distribution of sizes and density of ganglion cells in the retina of a porpoise, *Phocoena phocoena*. *Aquatic Mammals* 12: 95–102.
- Møhl, B. and Andersen, S. 1973. Echolocation: high-frequency component in the click of the Harbour Porpoise (*Phocoena ph.* L.). *Journal of the Acoustical Society of America* 54: 1368–1372.
- Moore, P. W. B., Dankiewicz, L. A. and Houser, D. S. 2008. Beamwidth control and angular target detection in an echolocating bottlenose dolphin (*Tursiops truncatus*). *Journal of the Acoustical Society of America* 124: 3324–3332.
- Murayama, T. and Somiya, H. 1998. Distribution of ganglion cells and

- object localizing ability in the retina of three cetaceans. *Fisheries Science* 64: 27–30.
- Murayama, T., Somiya, H., Aoki, I. and Ishii, T. 1995. Retinal ganglion cell size and distribution predict visual capabilities of Dall's porpoise. *Marine Mammal Science* 11: 136–149.
- Natoli, A., Peddemors, V. M. and Hoelzel, A. R. 2008. Population structure of bottlenose dolphins (*Tursiops aduncus*) impacted by bycatch along the east coast of South Africa. *Conservation Genetics* 9: 627–636.
- Norris, K. S., Prescott, J. H., Asa-Dorian, P. V. and Perkins, P. 1961. An experimental demonstration of echolocation behavior in the porpoise, *Tursiops truncatus* (Montagu). *Biological Bulletin* 120: 163–176.
- R Development Core Team. 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org/> (Accessed 16 May 2019).
- Tregenza, N. J. C., Berrow, S. D., Hammond, P. S. and Leaper, R. 1997. Harbour porpoise (*Phocoena phocoena* L.) by-catch in set gillnets in the Celtic Sea. *ICES Journal of Marine Science* 54: 896–904.
- Trippel, E. A., Strong, M. B., Terhune, J. M. and Conway, J. D. 1999. Mitigation of harbour porpoise (*Phocoena phocoena*) by-catch in the gillnet fishery in the lower Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 113–123.
- Verfuß, U. K., Miller, L. A. and Schnitzler, H.-U. 2005. Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*). *Journal of Experimental Biology* 208: 3385–3394.
- Verfuß, U. K., Miller, L. A., Pilz, P. K. and Schnitzler, H.-U. 2009. Echolocation by two foraging harbour porpoises (*Phocoena phocoena*). *Journal of Experimental Biology* 212: 823–834.
- Wagner, H. 1982. Flow-field variables trigger landing in flies. *Nature* 297: 147–148.
- Wood, F. G. and Evans, W. E. 1980. Adaptiveness and ecology of echolocation in toothed whales. In (Busnel R-G. and Fish J. F., eds.) *Animal Sonar Systems*, pp. 381–425. Plenum Press, New York.
- Yaman, S., von Fersen, L., Dehnhardt, G. and Güntürkün, O. 2003. Visual lateralization in the bottlenose dolphin (*Tursiops truncatus*): evidence for a population asymmetry? *Behavioural Brain Research* 142: 109–114.

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Appendix 1

Number of trials carried out per day

Number of trials/Day	Visual impediment	Control
6-Oct	1	0
7-Oct	1	4
8-Oct	4	18
9-Oct	4	12
10-Oct	2	11
11-Oct	3	14
12-Oct	3	7