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A kinematic study on (un)intentional imitation in bottlenose dolphins

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Keywords: imitation, mimicry, bottlenose dolphins, mirror neurons, automatic imitation, visuomotor priming.

1 Summary

2 The aim of the present study was to investigate the effect of observing other's movements on
3 subsequent performance in bottlenose dolphins. The imitative ability of non-human animals has
4 intrigued a number of researchers. So far, however, studies in dolphins have been confined to
5 intentional imitation concerned with the explicit request to imitate other agents. In the absence of
6 instruction to imitate, do dolphins (un)intentionally replicate other's movement features? To test
7 this, dolphins were filmed while reaching and touching a stimulus before and after observing
8 another dolphin (i.e., model) performing the same action. All videos were reviewed and segmented
9 in order to extract the relevant movements. A marker was inserted post-hoc via software on the
10 videos upon the anatomical landmark of interest (i.e. rostrum) and was tracked throughout the time
11 course of the movement sequence. The movement was analyzed using an in-house software
12 developed to perform two-dimensional (2D) post-hoc kinematic analysis. The results indicate that
13 dolphins' kinematics is sensitive to other's movement features. Movements performed for the
14 'visuomotor priming' condition were characterized by a kinematic pattern similar to that performed
15 by the observed dolphin (i.e., model). Addressing the issue of spontaneous imitation in bottlenose
16 dolphins might allow ascertaining whether the potential or impulse to produce an imitative action is
17 generated, not just when they intend to imitate, but whenever they watch another conspecific's
18 behavior. In closing, this will clarify whether motor representational capacity is a by-product of
19 factors specific to humans or whether more general characteristics such as processes of associative
20 learning prompted by high level of encephalization could help to explain the evolution of this
21 ability.

22 Introduction

23 The human capacity for imitation is well-known and is considered one of the hallmarks of human
24 cognition and culture (Meltzoff and Prinz, 2002). From infancy on, humans habitually copy
25 behaviours of every type across a variety of contexts (Meltzoff, 1996; Tomasello, 1999). For many
26 decades, those studying imitation in children and animals focused on *intentional* imitation because
27 it was thought that imitation must be controlled in order to play an important role in cognitive and
28 social development, and to mediate cultural inheritance (Heyes, 2009).

29 Given the central role of imitation in human cognitive evolution and development, it is perhaps not
30 surprising that a great amount of research has been devoted to ascertain whether this ability is
31 shared among non-human animals (Byrne and Bates, 2010; Fiorito and Scotto, 1992; Galef, 1988;
32 Leggio et al., 2000; Whiten and Ham, 1992).

33 A surprising aspect stemming from this body of work is that the animal most similar to humans in
34 imitative abilities may not be found among our closest relatives, but rather among cetaceans
35 (Herman, 2002). For instance, bottlenose dolphins (*Tursiops truncatus*) exhibit a prominent ability
36 to copy motor behaviours of conspecifics, humans, and other animals (Herman, 2002; Jaakkola et
37 al., 2010; Bauer and Johnson, 1994; Tyler and Saayman, 1973). So far, imitation in dolphins has
38 been chiefly investigated in terms of explicit request to imitate (e.g., Herman, 1980; Herman et al.,
39 1989; Marino, 2002; Kuczaj and Walker, 2006; Kuczaj et al., 2005). Rather, mimicry, imitative
40 behaviour that is *not intended* (Sturmer et al., 2000) and of which the imitator may be unaware
41 (Chartrand and Bargh, 1999), has received little attention. Unintentional imitation is a compatibility
42 effect in which the speed and/or accuracy of behavioral performance is modulated by the
43 relationship between the topographic features of an observed action and the observer's responses. In
44 the absence of instruction to imitate, movement observation *facilitates* execution of the observed
45 action. Such facilitation effects have been described in humans as a decrease in reaction time and an
46 increase in average velocity when an observed and a subsequently executed hand action matched
47 (i.e., *Visuomotor Priming*; see Craighero et al., 1998; Castiello et al., 2002; Edwards et al., 2003;

48 Heyes et al., 2005). It is generally agreed that unintentional imitation effects result from a process in
49 which action observation activates motor representations that are “similar” to the action observed
50 (Heyes, 2011). The interesting question is then: Does unintentional imitation depends on learned or
51 genetically prespecified, stimulus-response (S-R) connections? Single-unit recording indicates that
52 monkeys have mirror neurons in the premotor cortex, that is, cells that fire during observation and
53 execution of the same action (di Pellegrino et al., 1992; Gallese et al., 1996). Similarly, the areas of
54 the human brain that are activated by observation and execution of the same actions are sometimes
55 called the “mirror neuron system” (Gazzola and Keysers, 2009; Kilner et al., 2009). Many
56 developmental and comparative psychologists have suggested that nonhuman primates show
57 “mimicry” (Meltzoff and Moore, 1997; Tomasello, 1996) or “response facilitation” (Byrne and
58 Russon, 1998) because of simple, innate S-R links, and it is widely assumed that the perception–
59 action matching properties of “mirror neurons” are present at birth (Ferrari et al., 2009). On the
60 other hand, two theoretical accounts explain unintentional imitation as a by-product of learned
61 associations between perceptual and motor representations: the ideomotor theory of action control
62 (Massen and Prinz, 2009; Prinz, 2005) and the associative sequence learning model of imitation
63 (Catmur et al., 2009; Heyes, 2005). In this connection, the extent to which animals can imitate
64 might reflect representational capacity and is a matter of considerable importance (Whiten, 1996;
65 Suddendorf and Whiten, 2001; Kuczaj and Yeater, 2006). This is one reason why studying
66 unintentional imitation in dolphins is particularly significant. Conclusive evidence of unintentional
67 imitation in a species as phylo-genetically distant from primates as dolphins would play a pivotal
68 role in determining whether this motor representational capacity is a by-product of factors specific
69 to primates or whether more general characteristics such as processes of associative learning related
70 to a high level of encephalization could help to explain the evolution of this ability.
71 To investigate this issue, here we adapted a classic visuomotor priming paradigm. A dolphin “A”
72 observed another dolphin (i.e., model) performing a reach-to-touch (with the rostrum) action
73 towards a spherical object. Subsequently, the dolphin “A” performed the same action towards the

74 same object. A control condition in which the dolphin performed the same movement in the
75 absence of any motor priming was also included. On the basis of previous human findings based on
76 a similar paradigm (e.g., Edwards et al., 2003; Pierno et al., 2007), we hypothesize that if the
77 trailing dolphin is facilitated when primed by a dolphin model, then reach-to-touch movement
78 should exhibit a higher average velocity than when visuomotor priming does not occur. Conversely,
79 if no facilitation occurs, then primed and non-primed movements should not differ from a
80 kinematical perspective.

81

82 Materials and Methods

83 *Participants*

84 Two adult bottlenose dolphins (*Tursiops truncatus*, S. and L., male and female, 20 and 21 years
85 respectively) participated in the study. They swam in a pool of a round shape (20 meters in
86 diameter; capacity 1300 m³, surface 310 m² and maximum depth of 5 meters; Figure 1). The
87 experimental procedure for the dolphins was approved by the committee for animal research of the
88 University of Padova and adhered to the *Ethical Guidelines for the Conduct of Research on Animals*
89 *by Zoos and Aquariums* issued by the World Association of Zoos and Aquariums (WAZA).

90

91 *Stimulus and experimental set up*

92 The stimulus was a plastic ball (diameter 20 cm) attached to a pinnacle located to a fixed distance
93 of 10 mt from the starting position (Figure 2). Both the dolphins participating in this experiment had
94 already familiarized and played with the plastic ball attached to the pinnacle in previous years. We
95 purposely abstained from introducing a new stimulus in the pool area to avoid possible learning
96 effects.

97

98 *Video Recording technique*

99 A total of 12 hours of video footage was filmed during daylight hours between 10.00 a.m. and 12.00
100 p.m. in the time period between 27th of May and 7th of June, 2013. The video was filmed *ad libitum*

101 using a A GoPro camera Hero3 (Black Edition Wi-Fi compatible) fastened to a rigid trampoline
102 above the plane of motion. This procedure was utilized to guarantee a constant point of reference
103 during movements taking place on the plane perpendicular to the camera axis. A frame of reference
104 identifying X and Y axes as horizontal and vertical directions was manually set by an operator. In
105 order to calibrate the space of interest, a plank of 324 cm with a perpendicular bar at the distal end
106 (length 78 cm) was placed on three fixed points along the perimeter of the pool. A known length in
107 the camera's field of view and in the same plane as the movement was used as a measurement
108 reference unit.

109 *Procedure*

111 The trainer stood at the border of the pool facing the dolphins. Then by means of a fixed signal she
112 asked one of the dolphins (i.e., "A") to reach the stimulus and touch it with the rostrum (*Control*
113 condition; **Figure 2**). As soon as the stimulus was touched the trainer called the dolphin back to the
114 starting position by using a whistle. Then the trainer asked another dolphin (i.e., model) to reach
115 towards, touch the stimulus and then return to the starting position. Immediately after, the trainer
116 asked the dolphin "A" to perform again the reach-to-touch action (*Visuomotor Priming* condition).
117 **The "model dolphin" was kept oriented toward the platform by the trainer during performance of**
118 **dolphin "A" to prevent it from observing its movements. Nonetheless, to exclude the possibility that**
119 **in some trial "model" dolphin might be influenced by dolphin "A", all its data were removed from**
120 **the analysis.** The alternating sequence was repeated 10 times per daily session, with the dolphin "A"
121 always following the model (trials: 3,5,7,9,11) except for the control condition (trial 1). Both
122 dolphins acted as models and experimental subjects, in randomized sessions for 6 days. **Notably,**
123 **only one of them acted as experimental subject during each daily session, since only one of them**
124 **could perform the control condition (pre-observation of the model dolphin).**

125 *Data Processing*

126 Following data collection all videos were reviewed and segmented in order to extract the relevant

127 reach-to-touch movements. For the “visuomotor priming” condition only movements in which the
128 dolphin “A” observed the model performing the considered action before executing it were
129 considered for subsequent analysis. Two independent reviewers who were unaware of the study
130 rationale and blind to the experimental conditions scored each segment. They analysed the footage
131 frame-by-frame (frame duration: 20 milliseconds) using an in-house software developed to perform
132 post hoc kinematical analysis. Reliability between the two was quite high (Cohen's $\kappa = .86$). A
133 marker was placed post-hoc on each subject's rostrum. The starting position was defined as the
134 water area frontal to the trainer's platform at the border of the pool (2 m²). Movement onset was
135 defined as the time at which the tangential velocity of the marker crossed a threshold (5mm/sec)
136 and remained above it for longer than 500 msec. End of the movement was defined as the time at
137 which the rostrum touched the stimulus. Movement tracking procedures were then performed in
138 order to extract the kinematic parameter of interest. The analysis focused on the velocity profile to
139 evaluate how the observer's action changed following the observation of a model's movements
140 (Bisio et al., 2010). Average and Peak velocity, defined as the maximum velocity value occurring
141 between movement onset and offset, were then extracted. Modifications of mean velocity in
142 correspondence to changes of demonstrator's velocity are usually considered proof of the
143 occurrence of motion contagion.

144
145 *Statistics*

146 Two mixed-design repeated measures ANOVAs were carried out on average and peak velocity with
147 condition (control, visuomotor priming) as within-subject factor and dolphin identity (S., L.) as
148 between-subjects factor, to control for possible inter-individual differences. The strength and
149 direction of the linear relationship between average and peak velocity exhibited by dolphins “A”
150 and their models for the visuomotor priming condition was determined by means of a correlation
151 coefficient (Pearson's r). In particular, we correlated the average and peak velocity of each trial of
152 dolphin “A” to the just-observed movement of the model.

153 Results

154 Statistical analyses revealed a significant effect of condition for both average ($F_{(1,4)} = 8.67, p < 0.05,$
155 $\eta^2_p = 0.68$) and peak ($F_{(1,4)} = 7.94, p < 0.05, \eta^2_p = 0.67$) velocity. Dolphins were consistently faster
156 after the visuomotor priming than for the control condition (Table 1). Notably, the interaction
157 condition x dolphin identity was not significant ($p > 0.05$), suggesting that the priming influenced
158 the motor performance for both dolphins. Motor contagion effects were confirmed by the high level
159 of correlation between “A” dolphins and their models in terms of both average and peak velocity
160 (Table 1; see Figure 3 for a representative session).

161

162 Discussion

163 Collectively, these findings provide definite evidence that dolphins considered in this study showed
164 visuomotor priming effects, which might be due directly to activation by movement observation of
165 motor representations coding topographically similar responses. These findings, therefore, offer the
166 first convincing evidence that a non-primate species, the bottlenose dolphin, is capable of
167 unintentional imitation.

168 Our study reveals interesting similarities between the way dolphins and humans respond to action
169 observation. It suggests that action observation activates processes involved in action execution.
170 Synchronous behaviour exhibited by many dolphin species are classical examples of on-line motor
171 mimicry (Connor et al., 2000; Bauer and Harley, 2001). Rather our results, based on a *postponed*
172 facilitation effect, suggest a representational system that encodes information about other’s
173 behaviours in the same way it encodes information about one’s own behaviour (Gopnik, 1993).
174 These data fit well with theories assuming that the long-term S-R associations mediating
175 unintentional imitation are products of learning (Catmur et al., 2009; Heyes, 2005; Massen and
176 Prinz, 2009; Prinz, 2005). In this view we cautiously suggest that motor representations activated
177 following action observation might reflect an automatic resonance mechanism of motor structures
178 paralleling observed movements. This would imply that the emergence of mirror-like

179 manifestations are not a by-product of factors specific to primates, but instead might be attributable
180 to general processes of associative learning fostered by a high degree of encephalization and
181 cognitive ability. At the same time, the present results cannot exclude a speculative interpretation of
182 unintentional imitation in non-primate species. Mirror neurons fire when monkeys perform an
183 action, but also when the animal observe somebody else performing the same action (Gallese et al.,
184 1996; Rizzolatti et al., 2001). Following this discovery, studies have provided some evidence that
185 similar bimodal cells also exist in the human brain (Mukamel et al., 2010). Here, findings from our
186 study might indicate the presence of a similar mirror mechanism in dolphins too.

187 In conclusion, we suggest that even when dolphins do not intend to imitate, the perception of action
188 might activate the same neural (mirror neurons or mirror areas) or representational (common codes,
189 shared representations or vertical associations) structures that are involved in the production of the
190 perceived action. This might entail that in dolphins, rather than being distantly related by rules, the
191 perception and the execution of action depend on the same systems, and the potential (or impulse)
192 to produce an imitative action is generated not just when they intend to imitate, but whenever they
193 watch another dolphin's behavior.

194 To date, hypotheses about the evolution of unintentional imitation effects, as defined here, have
195 largely confined on primates. Our findings show a striking case of convergence in the face of
196 profound differences in neuroanatomical characteristics and evolutionary history. We are aware that
197 the issue of whether the unintentional imitation effects exhibited by dolphins rely on similar
198 mechanisms as primates remains partially unanswered, but this approach is promising and will shed
199 new light in the debate on the 'intentional' nature of imitative ability.

200 **Conflict of Interest Statement**

201 The authors declare that the research was conducted in the absence of any commercial or financial
202 relationships that could be construed as a potential conflict of interest.

203

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302 **Figure Captions**

303 Figure 1. Aerial view of the pool (20 meters in diameter; capacity 1300 m³, surface 310 m² and
304 maximum depth of 5 meters) and relative position of the target stimulus, video camera and trainer's
305 platform.

306 Figure 2. Schematic section of the pool and field of view of the video camera. The stimulus was a
307 plastic ball (diameter 20 cm) attached to a pinnacle located to a fixed distance of 10 mt from the
308 starting position.

309 Figure 3. Trial by trial Average Velocity (m/sec) recorded from the model (upper panel, a) and "A"
310 (lower panel, b) dolphins during a representative session (Day 1). (c) Linear relationship between
311 average velocity exhibited by dolphins "A" and model for the visuomotor priming condition
312 at Day 1.

Table 1. Average and Peak Velocity (m/sec) mean values recorded from the “A” and the “model” dolphins.

Session	<i>Average Velocity (m/sec)</i>				<i>Peak Velocity (m/sec)</i>			
	“A”		Model	<i>r</i>	“A”		Model	<i>r</i>
	Control	Visuomotor Priming			Control	Visuomotor Priming		
1	2.625	2.818	2.477	0.867*	8.062	8.781	8.409	0.941*
2	3.024	3.095	3.258	0.945*	6.345	7.071	9.740	0.879*
3	2.006	2.105	2.919	0.964**	7.387	8.062	9.662	0.983**
4	3.064	3.156	3.427	0.823	8.592	9.220	9.120	0.856
5	2.029	2.117	3.372	0.970**	8.902	9.220	12.042	0.858*
6	2.283	2.415	2.689	0.837	5.924	6.325	9.487	0.845

Pearson’s *r* indicate the correlation between each trial of dolphin “A” and the just-observed model movement. Asterisks indicate statistical significance (* $p < 0.05$; ** $p < 0.01$).

Figure 1.TIF

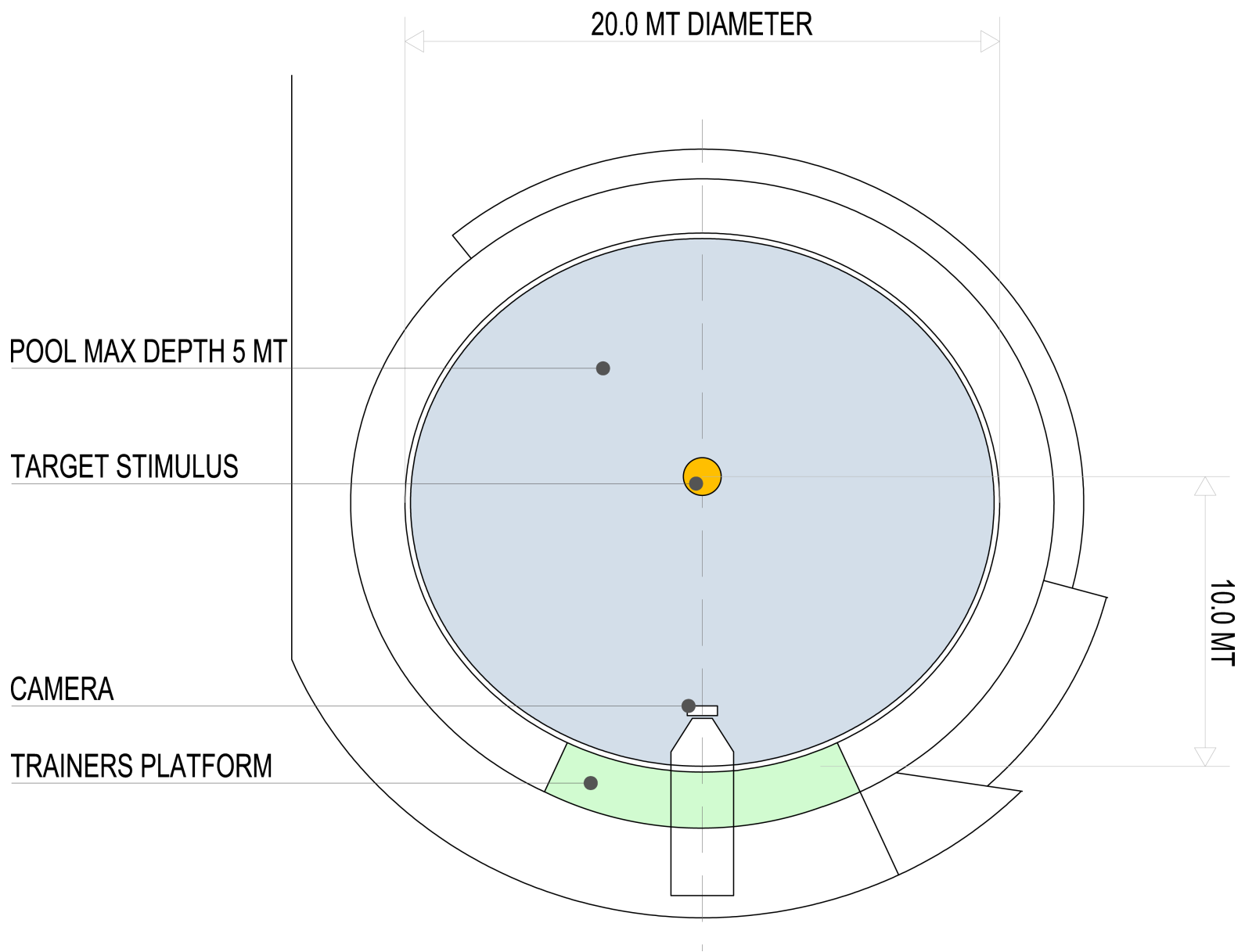


Figure 2.TIF

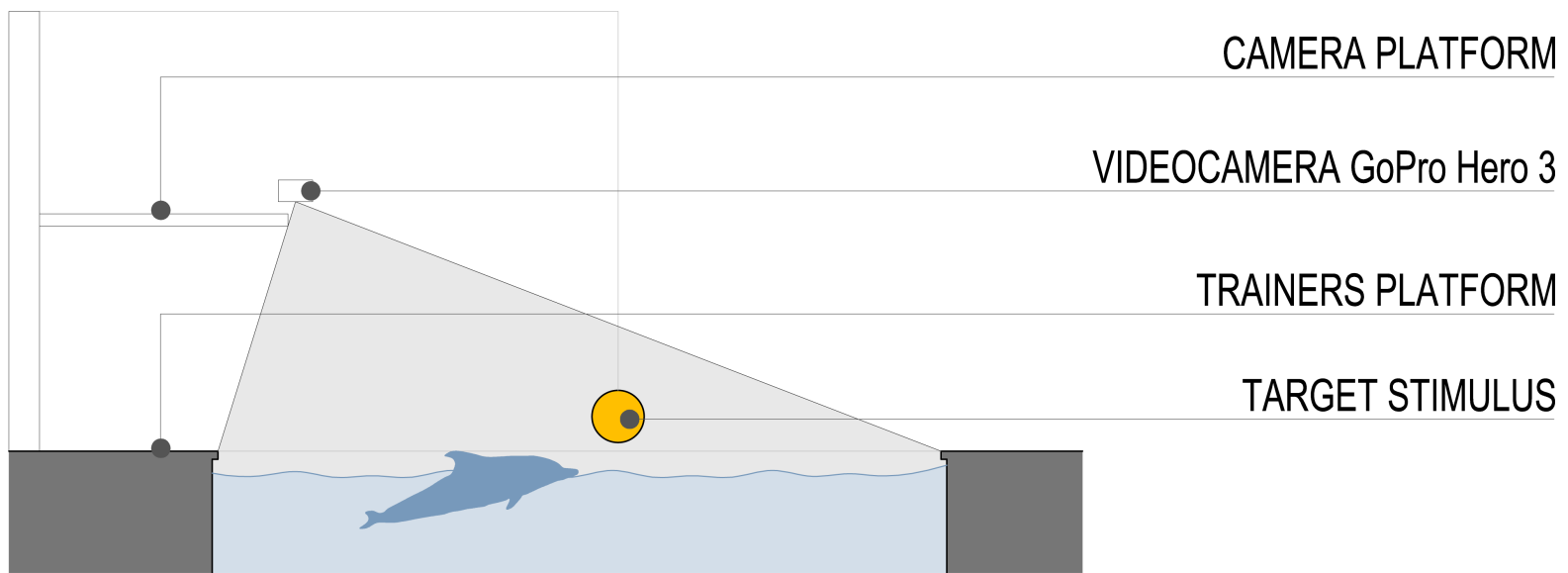


Figure 3.TIF

