

1 **Orcas remember what to copy: a deferred and interference-resistant imitation study.**

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12

13 **Abstract**

14 Response facilitation has often been portrayed as a “low level” category of social learning, because
15 the demonstrator’s action, which is already in the observer’s repertoire, automatically triggers that
16 same action, rather than induces the learning of a new action. One way to rule out response facilitation
17 consists of introducing a delay between the demonstrator’s behaviour and the observer’s response to
18 let their possible effects wear off. However, this may not rule out “delayed response facilitation” in
19 which the subject could be continuously "mentally rehearsing" the demonstrated actions during the
20 waiting period. We used a do-as-the-other-did paradigm in two orcas to study whether they displayed
21 cognitive control regarding their production of familiar actions by 1) introducing a delay ranging
22 from 60 to 150 sec between observing and producing the actions and 2) interspersing distractor (non-
23 target) actions performed by the demonstrator and by the subjects during the delay period. These two
24 manipulations were aimed at preventing the mental rehearsal of the observed actions during the delay
25 period. Both orcas copied the model’s target actions on command after various delay periods, and
26 crucially, despite the presence of distractor actions. These findings suggest that orcas are capable of
27 selectively retrieving a representation of an observed action to generate a delayed matching response.
28 Moreover, these results lend further support to the proposal that the subjects’ performance relied not
29 only on a mental representation of the specific actions that were requested to copy, but also flexibly
30 on the abstract and domain general rule requested by the specific “copy command”. Our findings
31 strengthen the view that orcas and other cetaceans are capable of flexible and controlled social
32 learning.

33 **Keywords**

34 Social learning mechanisms; deferred imitation; cognitive control; cetacean cognition; orca.

35

36 **Declarations**

37

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53 **Availability of data and material**

54 Data is uploaded as Supplementary Material in this initial submission.

55

56

57 **Code availability**

58 No code was used in relation to this paper.

59

60 **1. Introduction**

61 In many socially living species, individuals deploy a strong tendency to spontaneously copy the
62 actions currently or recently performed by other group members (Buttelmann et al. 2013; Fuhrman
63 et al. 2014; Nagasaka et al. 2013). This propensity to do as others do, or did, brings about several
64 behavioural and social consequences that can enhance the individuals' welfare and biological fitness
65 in those species. For example, by synchronously or diachronically reproducing the behaviour of
66 others, individuals can be more efficient when engaging in ecologically and socially fitness-relevant
67 activities which require interindividual coordination such as group hunting, group predator evasion,
68 and group defense of ecological or social resources (Handegard et al. 2012; Heyes 2013). This
69 proclivity to match the actions of others around you can favour the strengthening of social bonds
70 between in-group members and their greater willingness (and effectiveness) to behave pro-socially
71 towards one another (Cirelli 2018; Launay et al. 2016). Ultimately, this social learning can drive
72 intergroup differentiation and intragroup transmission of group-specific traditions and cultures (Dean
73 et al. 2016; van Schaik 2010).

74 Whereas the biologically adaptive function of social learning, i.e., acting like others in your
75 group, is generally well taken, the identification of, and consensus about, the actual psychological
76 mechanisms that underpin it have, however, been difficult to ascertain (Byrne 2002, 2009; Galeff
77 2013; Heyes 2021, Heyes and Ray 2000; Hoppitt and Laland 2008; Subiaul 2010; Tomasello 1990;
78 1996; Zentall 2006, 2011, 2022). There are at least three reasons why this has been so. First, far from
79 being a unitary process, social learning encapsulates a multiplicity of mechanisms which can engage
80 different cognitive resources. Second, social learning researchers have used different taxonomies to
81 name and define the alleged heterogeneity of the hypothesised cognitive foundations (Byrne 1994,
82 2002; Call and Carpenter 2002, 2003; Galef 1988; Galeff and Whiten 2017; Heyes 1994; Hoppitt and
83 Laland, 2008; Whiten and Ham 1992; Zentall 1996, 2001, 2022). Third, the theoretical frameworks
84 put forward to account for the various categories of social learning have often been silent about key
85 assumptions and have provided underspecified predictions difficult to test experimentally (Heyes
86 2021; Heyes and Ray 2000).

87 Many scholars define "Imitation" as instances when an observer copies the 'form' or topography
88 of a model's actions or body movements; that is, how parts of the body move relative to one another
89 (rather than copying the form of a caused tool or an object's movement, or copying only the end-state
90 emulation or outcome of an action; Heyes 2021; Whiten and Ham 1992; Whiten 2000; Whiten et al.
91 2004; 2009). Three major features commonly used to classify the various categories of imitation of a
92 demonstrator's actions are its perceptual opacity (Heyes 2001; Subiaul 2010; Zentall 2006, 2022), its

93 automaticity (Cracco et al. 2018; Heyes 2011) and its novelty (Byrne 2002, 2009; Heyes 2021; Zental
94 2022). Perceptual opacity refers to the extent of similarity between what the observer perceives when
95 the action is performed by the demonstrator, i.e., the visual input, and when it is performed by the
96 observer himself/herself, i.e., the motor output (Heyes and Ray 2000; Heyes 2001; Zental 2022). This
97 is one of the reasons why transitive (object-directed) actions are thought to be generally easier to
98 match than intransitive (non-object directed) actions (Heyes and Ray 2000; Bard 2007; Myowa-
99 Yamakoshi 2018; Zental 2022). Intransitive actions can also vary on perceptual opacity; for example,
100 facial gestures or head movements are less perceptually transparent than actions involving the
101 movement of appendages (Heyes and Ray 2000; Bard 2007; Myowa-Yamakoshi 2018). Although
102 automatic imitation is a major issue relevant to an understanding of perception and action in the
103 context of social functioning (Cracco et al. 2018; Heyes 2011; Myowa-Yamakoshi 2018), in the
104 present context automaticity refers to the extent of control and voluntariness of the observer's
105 response when he or she matches the actions performed by the demonstrator. The most convincing
106 demonstration of imitation involves the copying of another's action in the absence of any other
107 scaffolding information (e.g. the observable results or consequences of the model's action). Novelty
108 of demonstrated actions (i.e. production imitation) has become a cardinal feature to defining imitation
109 in narrower terms (Thorpe 1963; Boesch and Tomasello 1998), and distinguish it from other
110 supposedly less cognitively sophisticated forms of social learning, including, for example, response
111 facilitation where the presence of a demonstrator performing an act already in its repertoire, often
112 resulting in reward, increases the probability of an animal that sees it doing the same (Byrne 1994,
113 2002). Table 1 presents a selected list and definitions of social learning categories relevant to the
114 study reported here.

115 Overall, copying perceptually transparent, automatic and familiar actions is thought to be less
116 cognitively demanding than matching perceptually opaque, non-automatic and novel actions. Thus,
117 response facilitation is often portrayed as a cognitively "simple" category of social learning
118 (Carpenter and Call 2009), because the demonstrator's action is claimed to automatically trigger that
119 same action which is already in the observer's repertoire, rather than induce its acquisition. It is
120 generally assumed that such a process would have a transient effect on behaviour, which some authors
121 have suggested may be due to the fact that it is a product of priming (Byrne, 1994). This priming
122 could be explained by residual neural activity that remains for a short period of time after observation
123 of the demonstrator's actions. Alternatively, the transience may be due to the fact that as other,
124 mutually exclusive, actions are observed and the probability of their being performed increases, the
125 probability of the first action being performed will necessarily decrease (Hoppit and Laland 2008).
126 The same applies to "contagion" (see Table 1), which could be seen as an even simpler category of

127 social learning, as it implies the unconditioned and reflexive release of an instinctive behaviour that
128 requires no prior learning at all (e.g., yawning) (Hoppit and Laland 2008).

129 Accordingly, an important and contentious issue in imitation research is the extent that an
130 observer is capable of voluntarily controlling when and selecting which of several demonstrated
131 actions are to be matched (Huber et al. 2014). For example, Bandura (1969) proposed a distinction
132 between immediate imitation (response matching in which the demonstrator's response and the
133 observer's response occurred simultaneously or almost simultaneously) and observational learning.
134 He argued that the former was a simpler kind of imitation, as it is a released form of contagious
135 behaviour, a behaviour produced reflexively in response to a demonstration (i.e., genetically
136 predisposed). In contrast to immediate imitation, observational learning entails some kind of central
137 representation of the demonstrator's behaviour. According to Bandura, evidence for observational
138 learning comes from deferred imitation in which there is a delay between the observed demonstration
139 and the observer's performance (Zentall 2022). Therefore, one way of ruling out social learning
140 process that depends on immediate response matching as response facilitation consists of introducing
141 a delay between the demonstrator's performance and the observer's response. This category of social
142 learning would be a form of deferred (as opposed to immediate) imitation, and would entail the ability
143 to encode, retain and retrieve the memory of an observed action and then use it to match the model's
144 action after a time delay (Zentall 2006; 2022). Although it is unclear how long the facilitatory effect
145 of the response may last, and different researchers hold different criteria (for example, some authors
146 regard the terms short-term, sensory or perceptual memory as referring to the same construct), they
147 agree that one minute is a long enough delay interval to preclude a reflexive response based on both
148 sensory/perceptual memory (with a storage capacity of a few seconds at most) (see Laming and
149 Scheiwiller 1985) and short-term memory limited to a period of about 10 to 30 seconds (see Herrmann
150 et al. 2022; VandenBos 2007), which are commonly believed to be responsible for immediate
151 imitation (Zentall 2006; 2022; Zentall and Galef 2013). As for cetaceans, although it is true that it is
152 not yet known how high this limit could be, it must surely be similar to what has been demonstrated
153 in recent studies of short-term and working memory that have shown strong similarities between
154 humans and other animals (see Roberts and Santi 2017).

155 Deferred imitation has been researched in numerous studies with human infants (see Meltzoff
156 and Williamson 2013, for a review). These have mainly aimed at identifying the developmental age
157 at which the psychological processes believed to underlie deferred imitation, such as long-term
158 memory and mental representational systems, emerge in ontogeny. In contrast, studies of deferred
159 imitation in nonhumans have been relatively uncommon, have focused on few species and have
160 mostly analyzed transitive (object-directed) forms of social learning (great apes: Bering et al. 2000;

161 Bjorklund et al. 2000; 2002; Bjorklund and Bering 2003; Tomasello et al. 1993; Yunger and
162 Bjorklund 2004; dogs: Fugazza et al. 2016a; 2016b; Fugazza and Miklosi 2014; 2015). Instances of
163 deferred imitation in dolphins have also been described, although many of the matched actions were
164 transitive and were not collected via controlled experiments (see Kuczaj and Yeater 2006 and Yeater
165 and Kuczaj 2010 for reviews). In cetaceans, deferred matching of intransitive actions has, as far as
166 we know, only been studied in bottlenose dolphins (Herman 2002; Xitco 1988) . Dolphins were tested
167 with sets of delay intervals up to 80 sec, and it was found that the success rate of matched actions
168 decreased as the delay increased (dropping from 95% of correct copies at 25-sec delay to 74% after
169 a 60-sec delay and 59% after an 80-sec delay) (Xitco 1988). This decrease in action matching
170 performance both with 60 seconds delay (the short-term memory limit) and with 80 seconds delay
171 (only 20 seconds above the short-term limit), led some authors to suggest that the results could still
172 be explained by a response facilitation process (since the success of individuals' behavioral matching
173 was highly dependent on the immediacy of the observer's response to the model action; Hoppitt and
174 Laland 2008). Indeed, long delay intervals are expected to be challenging if the individual's ability
175 to copy relies on information stored in short-term memory (Hoppitt and Laland 2008; Zentall 2006).

176 Individuals could succeed in deferred imitation, but its performance still be regarded as
177 automatic, if during the retention intervals they could mentally rehearse the demonstrated action, they
178 were not exposed to any other demonstrated actions, or they were not behaviorally engaged. To rule
179 out this possibility, Herman and co-workers (1989, unpublished study cited in Herman 2002) carried
180 out a study of deferred imitation in one bottlenose dolphin that included the interspersing of distractor
181 actions that the subject was required to perform during the delay interval. They reported that the
182 dolphin was able to match the demonstrated actions accurately even after performing distractor
183 behaviors during the delay interval and claimed that this finding suggested that their performance
184 could rely on mental representations of the demonstrated actions. Unfortunately, Herman (2002) did
185 not provide any further details on the methods and results of this unpublished study, which makes
186 unfeasible any systematic evaluation of the strength of the evidence and of its potential implications.

187 The “Do as I do” paradigm, originally used by Hayes and Hayes (1952) to study a home raised
188 chimpanzee, has since been used to test immediate and deferred imitation in several species (great
189 apes: Call 2001; Custance et al. 1995; Hribar et al. 2014; dogs: Fugazza and Miklosi 2017; Topál et
190 al. 2006; dolphins: Bauer and Johnson 1994, Herman 2002; Xitco 1988; orcas: Abramson et al. 2013,
191 2018; belugas: Abramson et al. 2017). Individuals are first trained through operant conditioning
192 procedures to match their behavior to familiar actions performed by a demonstrator. Next, trained
193 individuals are tested with novel actions, situations, or demonstrators to see if they have learned the
194 abstract rule “do what (ever) the demonstrator does or did’ in immediate or deferred tests of imitation,

195 respectively. Importantly, in this second critical transfer phase, the observer is requested to copy a
196 demonstrated action in response to a specific gesturally or verbally signalled command (“Do this!”)
197 without any other scaffolding information (e.g., results-based cues). Interestingly, success in the
198 generalization of the Do-this command has been interpreted as evidence of the subject’s ability to
199 form a generalized behavior-copying concept, that is, some kind of concept of imitation (Herman
200 2002, 2010; Mercado and Scagel 2022;Whiten 2000; Zentall 2006). Table 2 presents a list of
201 representative Do-as-I-do studies of immediate/deferred imitation of familiar/novel,
202 transitive/intransitive actions in mammals relevant to the study reported here.

203 Among cetaceans, orcas are one of the main species along with bottlenose dolphins that stand out
204 for their group-specific hunting and foraging tactics and along with sperm whales for their vocal
205 repertoires (dialects) in the wild. Regarding their idiosyncratic foraging tactics, examples include
206 intentional beaching (Guinet 1991; Guinet and Bouvier 1995; Lopez and Lopez 1985), the “carousel
207 feeding’ technique (Similä and Ugarte 1993), or the “cooperative wave- washing behaviour” to take
208 seals off the ice floe (Pitman and Durban 2012; Smith et al. 1981) among others. As for their vocal
209 dialects matrilineal units or pods within a population have been documented to deploy a combination
210 of unique and shared call types (Deecke et al. 2000; Ford 1991; Miller and Bain 2000). All these
211 motor and vocal behaviors are believed to be transmitted via social learning, not only from mother to
212 offspring (vertical transmission), but also between matrilines (horizontal transmission) and do not
213 correlate with geographical distance (Filatova et al. 2012), therefore, they do not seem to be either
214 ecologically or genetically inherited and are often presented as model species of potential non-human
215 cultural traditions (Rendell and Whitehead 2001). Supporting this observational evidence, we have
216 already reported that orcas are capable of copying familiar and novel motor actions and sounds
217 demonstrated by conspecifics and humans, with remarkably positive results in both modalities, that
218 are comparable to that observed in dolphins tested under similar experimental conditions (Abramson
219 et al. 2013, 2018). However, the question of how much flexibility and cortical control of this ability
220 exists in this species and the presence of the capacity for deferred imitation of intransitive actions in
221 delphinids remains open.

222 The two goals of the present study of delayed imitation in the orca, were to 1) rule out response
223 facilitation and 2) to demonstrate the learning "on command" of the copying rule. For this purpose,
224 we used a “Do -as-the-other-did’ protocol that interspersed distracting (non-target) actions performed
225 by the demonstrator and by the subject during delay intervals ranging from 45 to 150 seconds.

226 Our rationale is that if subjects are able to copy intransitive actions demonstrated by a conspecific
227 after a delay interval, even when exposed to distractors during the retention interval, we may be able

228 to rule out “delayed object enhancement” (Hoppitt and Laland, 2008) and an “automatic and delayed”
229 response facilitation effect, explained by alternative explanations such as that the subjects adopted a
230 stereotyped posture or rehearsed mentally or motorically the target actions during the retention
231 interval (Herman 2002). This would allow us to conclude that the orcas are “in control” of their
232 matching response (since the subjects would only reproduce the action of the model that was indicated
233 by the “copy” command). Conversely, if they would copy the last behavior performed by the
234 demonstrator or the one performed by themselves (distractors), it would support the idea that the
235 matching response was “automatically” triggered, which could be explained by a response facilitation
236 effect.

237 In sum, by assessing the ability of orcas to non-automatically copy familiar, intransitive (body-
238 oriented) actions demonstrated on command under two cognitively challenging conditions (i.e.,
239 delayed copy and interspersing of distractors during the retention interval), we expect to lend further
240 support to the proposal that the subjects’ performance relied not only on a mental representation of
241 the specific actions that were requested to copy, but also flexibly on the domain general rule requested
242 by the specific “copy command”. Ultimately, we wanted to provide further experimental evidence
243 test that orcas and other cetaceans are capable of matching others’ conspecific behaviors in a flexible
244 and controlled way.

245

246 **2. Methods**

247 **(a) Subjects**

248 We tested two orca (*Orcinus orca*) subjects, a 15 year-old male named Inouk, and a 20-year-old
249 female named Wikie, both housed at Marineland Aquarium in Antibes, France. The conspecific
250 models, Moana and Keijo, were their calves, two males, five and two years old, respectively. All
251 subjects were born in the aquarium, were mother-reared, and lived together in a social group, with
252 access to five differently sized pools. All subjects had been trained for a variety of examination and
253 exercise behaviors with standard operant conditioning procedures and fish/tactile positive
254 reinforcement. The subjects had participated in a previous action imitation study (Abramson et al.
255 2013), so they were already trained with the “copy” command. Experimental sessions were done
256 between December 2017 and July 2021. During the experiments, subjects were tested in pairs in their
257 pools and were not food deprived. Testing was interrupted if subjects were distracted or disinclined
258 to participate.

259 **(b) Procedure**

260 Each testing session consisted of 1-3 blocks of 3 trials, lasting approximately 10–20 min altogether.
261 There were 1–4 sessions per day. The first two first trials of the testing sessions were our “baseline”
262 delay trials (delays of 5 and 15 sec respectively). These two baseline delays helped us to check if the
263 subjects were motivated to participate in the session and paid attention to the model. If they failed in
264 any one of them we cancelled the session and didn’t present the “test delay trial” (this occurred only
265 in one session with Inouk and in three sessions with Wikie). But if they succeeded, the test trial was
266 presented and scored as correct or incorrect.

267 The general experimental setup and procedures used were similar to those described in the previous
268 study on action imitation (Abramson et al. 2013). To run the experiments two trainers were needed,
269 namely, T_M and T_S (M for model and S for subject). They were positioned on different sides of a
270 wooden panel 2m long x 1.90 cm high placed in a position in which S and M could see each other
271 and their own trainer but could not see the other trainer’s commands. T_M was positioned on the right
272 side of the panel, and T_S on the left side; thus, the trainers were in a position from which they were
273 not able to see each other’s signals either (Abramson et al. 2013). The subjects were positioned in the
274 same pool and were rewarded with fish and with positive tactile and vocal signals whenever they
275 responded correctly. They received no reinforcement following errors. Reinforcement of the model
276 was not contingent upon the response of the subject. Positive reinforcement of the observer was given
277 only if his/her behavior after the “copy” command matched the action that had been demonstrated.
278 We used a set of 10 familiar behaviors extracted from the ones already tested in the previous study
279 of action imitation (Abramson et al. 2013). Importantly, all behaviors were body-oriented
280 (intransitive actions). Table 3 gives the complete list of the nine behaviors examined in this study and
281 its description. Delay intervals were measured by an alarm chronometer operated by the
282 experimenter.

283 The study comprised three phases. *Phase 1* involved retraining and reinforcing the subjects to
284 respond to the gesture-based command “copy” (“Do that!”) given by the trainer, which in the case of
285 Inouk had been used 7 years earlier in the previous study of action imitation (Abramson et al. 2013),
286 and in the case of Wikie had been used 2 years earlier in a previous study of vocal imitation
287 (Abramson et al. 2018), followed by the training of the subjects for deferred imitation. *Phase 2*
288 involved testing the subjects’ responses to the trainer’s copy command under a variable set of time
289 delays. Finally, *Phase 3* involved testing the subjects’ response to the trainer’s copy command with
290 the same variable delay intervals tested in the previous phase but now under two different distraction
291 conditions; in one of the conditions the demonstrator performed actions other than the target action
292 during the retention interval and in the other it was the observer himself who was asked to perform
293 distractor actions during the retention interval.

294 All sessions were videotaped by a video camera located above the tank in a position that provided
295 a full view of the two subject–trainer pairs and the entire tank.

296 **Phase 1. Preliminary training for deferred imitation:** Before the testing began, Inouk and Wikie
297 received a “training” period aimed first at “recalling” the copy command already trained (Abramson
298 et al. 2013, 2018), and then at teaching them that the “copy” command now referred to a particular
299 action, namely the target action, that had been demonstrated even if an interval elapsed between the
300 demonstration and the “copy” command. By using this procedure, we instructed the subjects that now
301 the “Do-it” signal turned into a “Do what the other *did!*” command referred to what had been
302 demonstrated before the scheduled delay interval. The first two training sessions began with eight
303 non-delay training trials, identical to those used previously in the immediate action imitation study
304 (Abramson et al. 2013), with both subjects producing 100% correct responses. Then we introduced a
305 delay interval before they were asked to display a copy of the demonstrated action. That is, the
306 subjects observed the demonstration of the target action and were requested to wait in the starting
307 position until they received the “copy” command action after the delay interval had elapsed. After the
308 T_S completed her command, the experimenter judged the subject's response and cued the Ts to
309 reinforce or not the subject. If the subject failed to respond, the procedure was repeated for a
310 maximum of two trials within each session. Training sessions divided into blocks of 4-16 trials
311 depending on the subjects’ attention and motivation, started with a duration of 3 seconds and
312 increased to 5 in the 2nd session and 15 in the 4th session. From the 6th session onwards, we used 5
313 seconds as our baseline delay interval and introduced a 30-sec delay interval. On a few occasions the
314 models performed other behaviors in addition to the ones they were asked to demonstrate.
315 Consequently, Ts “marked” the behavior that we wanted the subjects to copy by pointing with the
316 finger to the model while she/he was demonstrating the target behavior. Dolphins have been shown
317 to understand pointing (Pack and Herman 2004), and sometimes the orcas’ trainers had used a
318 pointing gesture with them in other training contexts.

319 Inouk succeeded in 100% of the trials (36/36) and Wikie in 88% of the trials (44/50) in their first
320 four sessions, however from the fifth session onwards their performance began to decrease,
321 sometimes failing even in the 5 seconds baseline delay trials that they had mastered previously. We
322 concluded that this drop in performance might be caused by the long duration of the sessions, which
323 negatively affected their attention and motivation. Therefore, we decided to shorten the duration of
324 the sessions and changed the configuration of the trial presentations to one up to four short blocks
325 interspersed by 5-minute (or longer) breaks. From the 15th session onwards, the subjects went through
326 the training sessions with this new protocol of each block consisting of three trials of different
327 behaviors with interval delays of 5, 15 and 30 sec respectively. When subjects reached a criterion of

328 more than 80% correct responses to 30 seconds delay trials in two consecutive sessions, they
329 advanced to phase 2.

330 **Phase 2. Deferred imitation (with no distraction) testing procedure:** This condition was tested with
331 one of the two subjects, Inouk. Testing sessions followed the same configuration as the last training
332 sessions consisting of one up to three blocks of three trials in which the two first trials were “baseline”
333 delay trials (with delays of 5 and 15 sec respectively). These two baseline delays helped us to check
334 if the subjects were motivated to participate in the session and paid attention to the model. Then, we
335 finished the block with a “test delay trial” in which the retention intervals were gradually increasing
336 from 60, to 90, 120 and 150 sec over successive sessions. Six trials of deferred imitation of different
337 behaviors chosen randomly without replacement from the list of nine familiar behaviors were run for
338 each one of these retention intervals (see Table 3 and Table 4). Only one trial of the longest delay
339 interval was presented within any block in any given session throughout the procedure.

340 **Control trials for behavior specific cues (“Clever Hans” control):** After the completion of the
341 variable delay testing procedure, four control trials were run to ensure that the subjects’ correct
342 responses were not based on some procedural or behavioral artifact that cued the identity of the
343 demonstrated behavior after the completion of the delay interval. Prior to each trial during the control
344 sessions, the T_s closed his eyes and turned his body away from the demonstrator, to prevent him from
345 seeing the model's behavior. At the end of the variable delay interval, the experimenter verbally cued
346 the T_s to give the copy command to the subject. After Inouk's response, the T_s was cued by the
347 experimenter to either reinforce him for a correct response or prepare him for the next trial. Six control
348 sessions were run, using the same set of four delays--baseline delays after 5 s, 15 s, and the longest
349 delay tested, 150 s.

350

351 **Phase 3a. Deferred imitation with distraction (Model distracting) testing procedure:** This phase
352 was run with Inouk, the subject tested in phase 2. In this condition, the subject observed the
353 demonstration of the target action and was then distracted during the retention interval by asking the
354 demonstrator to perform a non-target action that the subject was not requested to copy. The non-target
355 actions were the same actions used in the Do as I Do training and testing extracted randomly from
356 the list (Table 3). The subject was then requested to continue waiting in the starting position until he
357 received the “copy” command to perform the target action. We began with two training sessions with
358 30 seconds distraction trials as the longest delay. Testing involved the subject’s response to the T_s’s
359 copy command with the same variable delay intervals tested in the previous phases (from 45, to 60,

360 90, 120 and 150 sec over successive sessions), but now, with the potential interference of the non-
361 target action that the model also performed during the retention time.

362 The use of this type of distraction during the retention interval (the model performing non-target
363 actions) required the subject to respond specifically to the target “pointed” behavior we wanted him
364 to copy, thus controlling for his automatic response to the copy command, so that the ability to
365 voluntarily control what to imitate of the demonstrated actions after an interval can be tested.

366 ***Phase 3b. Deferred imitation with distraction (Observer distracting) testing procedure:***

367 This phase was run with Wikie, a subject not tested in previous phases, due to aquarium management
368 constraints that prevented the continuation of the experimental work with the subject tested in the
369 previous phases. In this condition she observed the demonstration of a familiar action chosen
370 randomly without replacement from the list of nine familiar actions previously selected. Then, before
371 the “copy” command was signaled, she was distracted during the retention interval by giving her a
372 different command to perform other different behaviors from the first demonstrated one. The use of
373 this type of distractions during the retention interval engaged the subject in a different activity, thus
374 preventing her from keeping her attention focused on the target action, so that the ability to encode
375 and recall the demonstrated action after an interval was tested. We run four training sessions with 30
376 sec distraction trials as the longest delay and then we tested the same retention intervals of 45 sec up
377 to 150 sec as in the previous variable delay phase.

378 **(c) Coding and data analysis**

379 Coding was done mainly by one experimenter, who watched the videos of each test trial and recorded
380 whether the subject’s action was a correct match of the demonstrator’s action. For reliability analysis,
381 a second experimenter coded 30% of the trials, watching just the subject’s actions but not the trainer’s
382 signal. Interobserver reliability was perfect (Cohen’s kappa coefficient for the observed behaviors
383 was 1, $p < 0.001$). Exact binomial tests for each phase and delay interval were performed to
384 investigate whether the individuals successfully copied the demonstrator’s actions above chance. To
385 estimate the probability of copying by chance, we adopt a rather conservative criterion, assuming that
386 chance performance for each subject in each trial would be $.10^{-1/[\text{number of different behavior}$
387 $\text{requested to be performed} + 1 \text{ (possibility of doing nothing)}]$ - . Note that this criterion is very
388 conservative, given that in theory, the subject had the possibility to select and perform any other
389 action from their repertoire requested usually as part of their training exercises, rather than just those,
390 namely, the target actions, requested in the test situation.

391 **3. Results**

392 ***Phase 1 Training***

393 The two subjects recalled the copy command (“Copy this!”) given by the trainer that they had last
394 used up to seven years earlier as indicated by their response in the first trial. Both subjects started
395 copying the demonstrator’s actions after the baseline delays (of 3, 5 and 15 sec) from the very
396 beginning of testing. The criterion required to reach correct performance, that is, 80% in two
397 consecutive sessions of 30 sec delay trials (that is, excluding the baseline delays of 3, 5 and 15 sec in
398 which both subjects were over 95% correct performance), was achieved by both subjects after eleven
399 30 sec trials (see Table 4).

400 ***Phase 2. Deferred imitation (with no distraction) testing procedure:***

401 Inouk performed above chance in every delay interval condition, producing full matches for 100% of
402 the demonstrated actions after delay intervals of 45, 60, 90 and 120 sec and 83% after the 150 sec
403 delay interval (all binomial tests: $ps < 0.001$) (see Table 4, and online resource video ESM_1.mpg;
404 video captions can be found in the online resource ESM_4.pdf).

405 **Control trials for behavior specific cues (“Clever Hans” control):**

406 Inouk’s performance was 100% correct in the four control trials, that is, when Inouk was asked to
407 match the action performed by the demonstrator after the longest delay interval, but while his trainer
408 had his/her eyes closed and back turned to the demonstrator, to prevent the trainer from seeing the
409 model's behavior.

410 ***Phase 3a. Deferred imitation with distraction (Model distracting) testing procedure:***

411 As in the previous phase, Inouk performed above chance in every delay interval, producing full
412 matches for 100% of the demonstrated actions after delays of 45, 60, and 120 sec and 83% after delay
413 interval of 90 sec (all binomial tests: $ps < 0.001$) (see Table 4 and online resource video ESM_2.mpg).

414 ***Phase 3b. Deferred imitation with distraction (Observer distracting) testing procedure***

415 Wikie also performed above chance in every delay interval condition, producing full matches for
416 100% of the demonstrated actions after delays of 60, and 120 sec, 83% after delay intervals of 45,
417 and 90 sec and 67% after delays of 150 sec (all binomial tests: $ps < 0.001$) (see Table 4 and online
418 resource video ESM_3.mpg).

419 **4. Discussion**

420 The two orcas participating in the present experimental study of social learning recalled in the first
421 trial the copy command (“Copy this!”), which they had last used up to seven years earlier, and
422 reproduced intransitive (body-oriented) actions demonstrated by a conspecific after delay intervals of

423 up to 150 sec. Their *deferred* matching performance was successful even when the subjects were
424 exposed to two types of *distractors* during the retention interval. Remarkably, their performance was
425 hampered neither by watching other non-target actions demonstrated by the model nor by non-target
426 actions that the subjects were asked to perform themselves during the retention interval. Their
427 successful performance in these cognitively challenging conditions rules out alternative explanations
428 such as that the subjects adopted a stereotyped posture or rehearsed mentally or motorically the target
429 actions during the retention interval (Herman 2002). It further indicates that the orcas' matching
430 ability was flexible and selective, two alleged signatures of cognitively complex social learning
431 (Hoppitt and Laland 2008; Huber et al. 2009).

432 Compared to *immediate* imitation, *deferred* imitation is argued to be more cognitively demanding
433 and another hallmark of complex socially mediated copying (Zentall and Galef 1988). The *length* of
434 some of the *delay intervals* used in the present study more than doubled the cut-off interval duration
435 of 60 sec that has been suggested to be sufficient to exclude a kind of automatic and reflexive
436 responding based on short-term perceptual memory and, therefore, the operation of social learning
437 mechanisms such as immediate imitation (Byrne 2009; Galef 2013; Heyes 2021; Heyes and Ray
438 2000; Hoppitt and Laland 2008) and automatic facilitative processes (Cracco et al. 2018; Heyes 2011;
439 Heyes and Ray 2000; Hoppitt and Laland 2008; Zentall 2006). That is, the subjects' matching
440 behaviour appeared to rely on the retrieval of an enduring mental representation of the target action.
441 Unlike the dolphins in Xitco's (1988) study of deferred imitation, whose rate of correct matching
442 decreased as delay intervals increased (i.e., 95% after 25 sec; 74% after 60 sec; 59% after 80 sec),
443 the orcas' rate of successful behavioral matching remained at very high levels for longest delays, not
444 declining with delay intervals up to 120 seconds (i.e., 100% after 60, 90 and 120 sec, 83% after 150
445 sec).

446 Although it is difficult to know what is the "limit of sensory or perceptual memory" in orcas, the
447 results obtained in the distraction conditions rule out a delayed version of the traditional response
448 facilitation, that is, that the subjects were continuously "mentally rehearsing" the demonstrated
449 actions during the waiting period, which could have extended the perceptual memory substantially.
450 The inclusion of distractors, in particular distractor 1 (model distracting condition), was critical to
451 test for a deferred response facilitation effect, which could be argued to operate only if the observer
452 copied the last behaviour he have seen or that the model had demonstrated only one behaviour, that
453 then would be "automatically triggered" with the mere presence of the model. This effect is discarded,
454 however, when the action that the model has recently demonstrated [the distractor] does not
455 correspond to the target one that the observer correctly performed in the presence of the model.

456 The distractors conditions were also critical to test for the “control” of the matching response
457 since the subjects only reproduced the model’s action that was indicated with the “copy” command
458 (Hoppitt and Laland 2008). Several imitation theorists (e.g., Whiten 2000; Zentall 2006) and
459 researchers of dolphin imitation (e.g., Herman 2002; Xitco 1988) have stated that the deployment of
460 “copying on command” might suggest the ability to generalize from copying a couple of familiar
461 actions to several actions, including novel ones, in response to a specific “copy signal”. This has been
462 interpreted as acquiring a general and abstract concept or meta-representation of imitation (Mercado
463 and Scagel 2022), a capacity that has been suggested to be a fundamental prerequisite for the
464 evolution of the human capacity to have some concept or awareness of cultural conventions (Whiten
465 2000). In particular, distractor 2 (observer distraction) was critical to test for the “control” of the
466 matching response since the subjects only reproduced the model’s action that was indicated with the
467 “copy” command and not the last they either saw being performed by the demonstrator or was
468 performed by themselves. Accordingly, the positive results obtained in the present study suggest that
469 this flexibility may rely on some kind of representation or conceptual learning of the action “copy
470 this, and only this, action” that may underpin the generalization of this trained “copy what the other
471 has done“ signal to different behaviours without additional training (Herman 2002; Hoppitt and
472 Laland 2008; Kuczaj and Yeater 2006; Mercado and Scagel 2022; Whiten 2000; Xitco 1988). The
473 mechanisms underlying flexible repetition of observed actions after a delay, even with distraction
474 during the retention intervals, provides further evidence that a “repeating” or “imitation” rule was
475 learned that can be applied to many different actions. The generalization of this copy signal in these
476 deferred imitation tests provided in this study strengthen that the orcas were relying on a flexible,
477 domain general, relational “copy what the other is doing or have done” concept and even further,
478 "copy when I tell you and what I tell you and not something else" rule, and not an associatively
479 learned concrete perceptual-motor representation or skills (see Mercado and Scagel 2022). Therefore,
480 this finding gives further support to the notion that they were relying on a “mental representation”
481 (Zentall and Galef 2013), not only of the specific actions that were requested to copy, but also of the
482 abstract and general rule requested by the specific command “copy what the other is doing”.

483 Previous comparative work on deferred imitation has mostly focused on the copying of *transitive*,
484 object-oriented, actions (great apes: Bering et al. 2000; Bjorklund et al. 2000; Bjorklund et al. 2002;
485 Bjorklund and Bering 2003; Tomasello et al. 1993; Yunger and Bjorklund 2004; dogs: Fugazza et al.
486 2016a, 2016b; Fugazza and Miklosi 2014, 2015; see Table 2). It is generally agreed that copying
487 transitive actions is less cognitively demanding than imitating intransitive actions (Heyes and Ray
488 2000; Subiaul 2007, 2010; Zentall 2003, 2011). Indeed, in the latter the subject must copy the body
489 movements without any object in the environment that helps to “enhance” the memory or guide the

490 action to be displayed (Tennie et al 2009). In contrast, Herman’s study (2002) of deferred imitation
491 in dolphins and the present work of deferred imitation in the orca involved intransitive, body-oriented,
492 actions. The difficulty of reproducing intransitive actions is further increased when a delay is
493 introduced between observation and reproduction. Therefore, the present study’s results on deferred
494 imitation of intransitive actions provide remarkably solid evidence to rule out “delayed object
495 enhancement” (Hoppitt and Laland, 2008) and automatic response facilitation in a non-human animal,
496 as: a) no environmental cue was present (other than the action of the demonstrator itself), b) two types
497 of control conditions were introduced (i.e., the demonstrator and the observer performed non-target,
498 distractor actions during the retention interval) and c) the success rate of matching did not decline
499 significantly, not even at delays almost twice as long as the longest delay tested by Xitco (1988) in
500 the bottlenose dolphin.

501 Overall, our results support that imitation can occur both in the copying of new actions
502 (Abramson et al 2013) and in the copying of familiar ones in new contexts. The problem with familiar
503 actions is that sometimes it is not possible to distinguish between both mechanisms, imitation and
504 facilitation (see Byrne and Russon 1998), whereas when copying novel actions, facilitation of the
505 response can be ruled out. The aim of this work has been to rule out response facilitation by
506 introducing controls to assess the persistence of a mental representation of the behaviour to be copied
507 and the observer’s control (voluntariness) to execute it as required. Similarly, Jaakkola et al., (2010)
508 demonstrated that bottlenose dolphins were able to imitate familiar behaviours of another dolphin but
509 in a blindfolded (i.e., wearing eyecups) condition. Moreover, the blindfolded echolocation
510 dramatically increased when copying a human as compared to other dolphins, suggesting that the
511 dolphin’s imitation was under control and not automatically elicited (Jaakkola et al. 2013).

512 Studies of immediate and deferred imitation of several species of cetaceans, including bottlenose
513 dolphins (Herman 2002; Xitco 1988), belugas (Abramson et al. 2017), and orcas (Abramson et al.
514 2013, 2018, this study) have all highlighted their propensity to engage in actions requiring high levels
515 of interindividual behavioural synchrony and coordination in several contexts, particularly during
516 hunting (Lopez and Lopez 1985; Pitman and Durban 2012; Visser et al. 2008). Orcas are large-
517 brained, socially complex, and highly cooperative water-dwelling mammals (Marino 2022). They
518 have also been reported to possess group-specific behavioral traditions and vocal dialects
519 hypothesized to be socially learned (Filatova et al. 2015). Several researchers have highlighted the
520 notably conservative nature of the orcas’ traditions or “cultures”, where innovation is typically
521 infrequent, but can spread very fast once it emerges (Barrett-Lennard and Heise 2007; Whitehead and
522 Rendell 2014). This strong proclivity to copy what others are doing and to conform to the actions of
523 their group members may be a key driver of intergroup differentiation and intra-group identity (Byrne

524 2009; Meltzoff and Decety 2003), ultimately resulting in the reproductive isolation of sympatric
525 groups and incipient speciation (Riesch et al. 2012).

526 **Conclusion**

527 Over the years, researchers have documented the existence of a diversity of social learning
528 mechanisms in the animal kingdom and created taxonomies that implicitly or explicitly classify them
529 in terms of the sophistication of their hypothesized underlying cognitive processes. Traditionally,
530 social learning mechanisms that result in the acquisition of novel actions (production imitation) are
531 considered more cognitively complex than those that merely increase the likelihood of reproducing
532 familiar actions (e.g., response facilitation). In this study, however, we provide experimental evidence
533 that challenges this well-entrenched idea by showing that copying familiar actions, which is
534 considered a “low-level” form of social learning compared to copying novel actions, may in fact not
535 be as simple. Our findings are inconsistent with the notion that orcas displayed response facilitation
536 because they showed considerable cognitive control over the reproduction of observed actions. Recall
537 that response facilitation is thought to trigger responses automatically, e.g., via priming. In contrast,
538 our findings suggest that orcas can use a controlled form of imitation, one that entails the voluntary
539 production of familiar actions, as opposed to automatic movements or non-intentional actions; this is
540 a “high level” cognitive component that most authors tend to attribute only to cases of imitation of
541 novel actions. However, learning a novel action is only one indicator of cognitive sophistication. As
542 Tomasello (2022 pp 1 and pp 5) has recently stated: “the issue in animal cognition evolution if we
543 are concerned with the psychological mechanisms by which organisms generate their actions, is not
544 about complexity of the behaviour itself or whether is innate or learned, but rather the degree to which
545 the behaviour performed is under the individual’s control.

546 The present study adds further information on the behavioural and cognitive profile of this
547 species by showing that orcas are capable of selectively retrieving an enduring representation of an
548 observed action to generate a delayed matching response which is resistant to distractor actions and
549 which is done on command. This supports the notion that the orcas possess a flexible social learning
550 capacity that must underpin the generalization of the trained “copy what the other is doing” signal to
551 different behaviours, even if distracted by other non-target actions during the delay interval, which
552 excludes reflexive and automatic social learning mechanisms based only on short-term and perceptual
553 memory. Still our results should be interpreted with caution, as the sample size is small.
554 Consequently, further experimental studies on cetaceans are needed to test this study’s conclusions
555 and elucidate the nature of the orca’s imitative skills.

556 Taken together, the findings from this experimental study suggest that the orcas may have the
557 potentiality to control from whom, what and when matching others’ actions. This capacity of orcas

558 to copy under voluntary control what others are doing would be consistent with the body of
559 observations on group-specific behavioural traditions and vocal dialects, synchronized behaviour,
560 and sophisticated cooperative strategies and could be at the base of the conformity to the group's
561 normative traditions, documented in this species (Barrett-Lennard and Heise 2007; Lopez and Lopez
562 1985; Filatova et al. 2015; Pitman and Durban 2012; Visser et al. 2008; Whitehead and Rendell 2014).

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Table 1. Taxonomy of selected social learning categories

Aspect copied	Novelty	Mechanism	Definition	
Not specified		Social facilitation	The mere presence of a demonstrator makes certain behaviour more likely, influencing the observer's behaviour and learning processes	Zajonc 1965
Not specified		Local enhancement	The demonstrator presence at a particular location, attracts the observer's attention to visit that location	Thorpe 1963
Not specified		Stimulus enhancement	The demonstrator's behavior (or its products) draws attention and exposes the observer to a particular stimulus with which the demonstrator was interacting	Heyes 1994
Not specified		Observational Learning	An organism copies an improbable action or action-outcome that it has observed	Zentall 2012
Action	Familiar	Contagion	The spread of an instinctive behavior across individuals caused by the performance of the same behavior in the demonstrator	Thorpe 1963
Action	Familiar	Response facilitation	The presence of a demonstrator performing an act that is already in the observer repertoire (often resulting in reward for the demonstrator) increases the probability of the observer doing the same.	Byrne 1994
Action	Familiar	Imitation	An observer copies the form or topography of a demonstrator's <i>familiar</i> actions or body movements	Adapted from Whiten et al. 2004 and Heyes 2021
Action	Familiar	Contextual imitation	Learning to employ an action already in the observer repertoire, in different circumstances	Bates & Byrne (2010)
Action	Familiar	Immediate Imitation	The demonstrator's response and the observer's response occurred simultaneously or almost simultaneously.	Bandura 1969
Action	Familiar	Deferred Imitation	Imitation of the observed action of a demonstrator after a variable time interval has elapsed	Zentall 2006, 2012
Action	Novel	Production imitation	After observing a demonstrator performing a novel action, a novel sequence or a combination of actions that is not in the observer's own repertoire, the likelihood of the observer performing that novel action, sequence or combination of actions increases	Byrne 2002

Outcome	Novel	Emulation	The individual observing and learning some affordances or changes of state of the inanimate world as a result of the behavior of another animal, and then using what it has learned in devising its own behavioral strategies	Tomasello 1990
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* Italics are ours.

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Table 2. Representative Do-as-I-do studies of immediate/deferred imitation of familiar/novel, transitive/intransitive actions in mammals.

Novelty	Timing	Type	Species	Reference
Familiar	Immediate	Transitive	Chimpanzee	Hribar et al. 2014
			Orangutan	Call 2001
			Dog	Topal et al. 2006
		Intransitive	Chimpanzees	Bard 2007; Myowa-Yamakoshi 2018
			Dog	Topal et al. 2006
	Deferred	Transitive	Dolphin	Bauer and Johnson 1994; Jaakkola et al. 2010; 2013
			Beluga	Abramson et al. 2017
			Orca	Abramson et al. 2018
		Intransitive	Dolphin	Herman 2002; Xitco 1988
			Orca	This Study
Novel	Immediate	Transitive	Chimpanzee	Hribar et al., 2014; Custance et al. 1995
			Dog	Topal et al. 2006; Huber et al. 2009
		Intransitive	Dolphin	Herman 2002; Xitco 1988
	Orca		Abramson et al. 2013; 2018	
	Deferred		Transitive	Dog
			Intransitive	

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Table 3 Behaviors tested

Behaviour	Description
Squirt (SQ)	Split water out of the surface
Song (SO)	Emit a whistling sound (vocalize out of the water)
Tapec caudal (TC)	Slap tail continuously on water surface
Roll over (RO)	Turn over, ventral side up, and maintain the position
Houla (HU)	Rise vertically on water, half of the body on the surface, and roll continuously in 360
Pec splash (PS)	Pectoral fin out of water while keeping it motionless a few seconds and then slap once and heavily on the water
Fluke wave (FW)	Dive downward to a vertical position with tail fluke protruding from the water and shaking it
Yes (YES)	Nods head down up and down
Tongue out (TO)	With the head out of the water take out (showing) the tongue

Every behaviour is described taking as the starting point the animal facing the trainer while lying horizontally on the water's surface and in perpendicular position to the pool wall

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Table 4. Percentage of deferred copies (n = 6) for each delay interval and test condition.

	INOUK	WIKIE
<i>Phase 2: No distraction</i>		
Delay		
45	100	
60	100	
90	100	
120	100	
150	83	
<i>Phase 3a: Model distracting</i>		
Delay		
45	100	
60	100	
90	83	
120	100	
<i>Phase 3b: Observer distracting</i>		
Delay		
45		83
60		100
90		83
120		100
150		67

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