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ORIGINAL PAPER

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

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Abstract

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

Keywords Social learning mechanisms · Deferred imitation · Cognitive control · Cetacean cognition · Orca

Introduction

In many socially living species, individuals deploy a strong tendency to spontaneously copy the actions currently or recently performed by other group members (Buttelmann et al. 2013; Fuhrmann et al. 2014; Nagasaka et al. 2013). This propensity to do as others do, or did, brings about several behavioral and social consequences that can enhance the individuals' welfare and biological fitness in those species. For example, by synchronously or diachronically reproducing the behavior of others, individuals can be more efficient when engaging in ecologically and socially fitness-relevant activities which require interindividual coordination such as group hunting, group predator evasion, and group defense of ecological or social resources (Handegard et al. 2012; Heyes 2013). This proclivity to match the actions of others around you can favor the strengthening of social bonds between in-group members and their greater willingness (and effectiveness) to behave pro-socially towards one another (Cirelli

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2018; Launay et al. 2016). Ultimately, this social learning can drive intergroup differentiation and intra-group transmission of group-specific traditions and cultures (Dean et al. 2018; van Schaik 2010).

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

Many scholars define "Imitation" as instances when an observer copies the 'form' or topography of a model's actions or body movements; that is, how parts of the body move relative to one another (rather than copying the form of a caused tool or an object's movement, or copying only the end-state emulation or outcome of an action; Heyes 2021; Whiten and Ham 1992; Whiten 2000; Whiten et al. 2004; 2009). Three major features commonly used to classify the various categories of imitation of a demonstrator's actions are its perceptual opacity (Heyes 2001; Subiaul 2010; Zentall 2006, 2022), its automaticity (Cracco et al. 2018; Heyes 2011) and its novelty (Byrne 2002, 2009; Heyes 2021; Zentall 2022). Perceptual opacity refers to the extent of similarity between what the observer perceives when the action is performed by the demonstrator, i.e., the visual input, and when it is performed by the observer himself/herself, i.e., the motor output (Heyes and Ray 2000; Heyes 2001; Zentall 2022). This is one of the reasons why transitive (object-directed) actions are thought to be generally easier to match than intransitive (non-object directed) actions (Heyes and Ray 2000; Bard 2007; Myowa-Yamakoshi 2018; Zentall 2022). Intransitive actions can also vary on perceptual opacity; for example, facial gestures or head movements are less perceptually transparent than actions involving the movement of appendages (Heyes and Ray 2000; Bard 2007; Myowa-Yamakoshi 2018). Although automatic imitation is a major issue relevant to an understanding of perception and action in the context of social functioning (Cracco et al. 2018; Heyes 2011; Myowa-Yamakoshi 2018), in the present context, automaticity refers to the extent of control and voluntariness of the observer's response when he or she matches the actions performed by the demonstrator. The most convincing demonstration of imitation involves the copying of another's action in the absence of any other scaffolding information (e.g., the observable results or consequences of the model's action). Novelty of demonstrated actions (i.e., production imitation) has become a cardinal feature to defining imitation in narrower terms (Thorpe 1963; Boesch and Tomasello 1998), and distinguish it from other supposedly less cognitively sophisticated forms of social learning, including, for example, response facilitation where the presence of a demonstrator performing an act already in its repertoire, often resulting in reward, increases the probability of an animal that sees it doing the same (Byrne 1994, 2002). Table 1 presents a selected list and definitions of social learning categories relevant to the study reported here.

Overall, copying perceptually transparent, automatic and familiar actions is thought to be less cognitively demanding than matching perceptually opaque, non-automatic and novel actions. Thus, response facilitation is often portrayed as a cognitively "simple" category of social learning (Carpenter and Call 2009), because the demonstrator's action is claimed to automatically trigger that same action which is already in the observer's repertoire, rather than induce its acquisition. It is generally assumed that such a process would have a transient effect on behavior, which some authors have suggested may be due to the fact that it is a product of priming (Byrne 1994). This priming could be explained by residual neural activity that remains for a short period of time after observation of the demonstrator's actions. Alternatively, the transience may be due to the fact that as other, mutually exclusive, actions are observed and the probability of their being performed increases, the probability of the first action being performed will necessarily decrease (Hoppitt and Laland 2008). The same applies to "contagion" (see Table 1), which could be seen as an even simpler category of social learning, as it implies the unconditioned and reflexive release of an instinctive behavior that requires no prior learning at all (e.g., yawning) (Hoppitt and Laland 2008).

Accordingly, an important and contentious issue in imitation research is the extent that an observer is capable of voluntarily controlling when and selecting which of several demonstrated actions are to be matched (Huber et al. 2014). For example, Bandura (1969) proposed a distinction between immediate imitation (response matching in which the demonstrator's response and the observer's response occurred simultaneously or almost simultaneously) and observational learning. He argued that the former was a simpler kind of imitation, as it is a released form of contagious behavior, a behavior produced reflexively in response to a demonstration

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 behavior more likely, influencing the observer's behavior 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 *familiar* 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 and 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)

[*] Italics are ours

(i.e., genetically predisposed). In contrast to immediate imitation, observational learning entails some kind of central representation of the demonstrator's behavior. According to Bandura, evidence for observational learning comes from deferred imitation in which there is a delay between the observed demonstration and the observer's performance (Zentall 2022). Therefore, one way of ruling out social learning process that depends on immediate response matching as response facilitation consists of introducing a delay between the demonstrator's performance and the observer's response. This category of social learning would be a form of deferred (as opposed to immediate) imitation, and would entail the ability to encode, retain and retrieve the memory of an observed action and then use it to match the model's action after a time delay (Zentall 2006, 2022). Although it is unclear how long the facilitatory effect of the response may last, and different researchers hold different criteria (for example, some authors regard the terms short-term, sensory or perceptual memory as referring to the same construct), they agree that 1 min is a long enough delay interval to preclude a reflexive response based on both sensory/perceptual memory (with a storage capacity of a few seconds at most) (see Laming and Scheiwiller 1985) and short-term memory limited to a period of about 10 to 30 s (see Herrmann et al. 2022; VandenBos 2007), which are commonly believed to be responsible for immediate imitation (Zentall 2006, 2022; Zentall and Galef 2013). As for cetaceans, although it is true that it is not yet known how high this limit could be, it must surely be similar to what has been demonstrated in recent studies of short-term and working memory that have shown strong similarities between humans and other animals (see Roberts and Santi 2017).

Deferred imitation has been researched in numerous studies with human infants (see Meltzoff and Williamson

2013, for a review). These have mainly aimed at identifying the developmental age at which the psychological processes believed to underlie deferred imitation, such as long-term memory and mental representational systems, emerge in ontogeny. In contrast, studies of deferred imitation in nonhumans have been relatively uncommon, have focused on few species and have mostly analyzed transitive (object-directed) forms of social learning (great apes: Bering et al. 2000; Bjorklund et al. 2000, 2002; Bjorklund and Bering 2003; Tomasello et al. 1993; Yunger and Bjorklund 2004; dogs: Fugazza et al. 2016a, b; Fugazza and Miklosi 2014; 2015). Instances of deferred imitation in dolphins have also been described, although many of the matched actions were transitive and were not collected via controlled experiments (see Kuczaj and Yeater 2006 and Yeater and Kuczaj 2010 for reviews). In cetaceans, deferred matching of intransitive actions has, as far as we know, only been studied in bottlenose dolphins (Herman 2002; Xitco 1988). Dolphins were tested with sets of delay intervals up to 80 s, and it was found that the success rate of matched actions decreased as the delay increased (dropping from 95% of correct copies at 25-s delay to 74% after a 60-s delay and 59% after an 80-s delay) (Xitco 1988). This decrease in action matching performance both with 60-s delay (the short-term memory limit) and with 80-s delay (only 20 s above the short-term limit) led some authors to suggest that the results could still be explained by a response facilitation process (since the success of individuals' behavioral matching was highly dependent on the immediacy of the observer's response to the model action; Hoppitt and Laland 2008). Indeed, long-delay intervals are expected to be challenging if the individual's ability to copy relies on information stored in short-term memory (Hoppitt and Laland 2008; Zentall 2006).

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

The "Do as I do" paradigm, originally used by Hayes and Hayes (1952) to study a home raised chimpanzee, has since been used to test immediate and deferred imitation in several species (great apes: Call 2001; Custance et al. 1995; Hribar et al. 2014; dogs: Fugazza and Miklosi 2017; Topál et al. 2006; dolphins: Bauer and Johnson 1994; Herman 2002; Xitco 1988; orcas: Abramson et al. 2013, 2018; belugas: Abramson et al. 2017). Individuals are first trained through operant conditioning procedures to match their behavior to familiar actions performed by a demonstrator. Next, trained individuals are tested with novel actions, situations, or demonstrators to see if they have learned the abstract rule "do what (ever) the demonstrator does or did' in immediate or deferred tests of imitation, respectively. Importantly, in this second critical transfer phase, the observer is requested to copy a demonstrated action in response to a specific gesturally or verbally signaled command ("Do this!") without any other scaffolding information (e.g., results based cues). Interestingly, success in the generalization of the Do-this command has been interpreted as evidence of the subject's ability to form a generalized behavior-copying concept, that is, some kind of concept of imitation (Herman 2002, 2010; Mercado and Scagel 2022; Whiten 2000; Zentall 2006). Table 2 presents a list of representative Do-as-I-do studies of immediate/deferred imitation of familiar/novel, transitive/intransitive actions in mammals relevant to the study reported here.

Among cetaceans, orcas are one of the main species along with bottlenose dolphins that stand out for their group-specific hunting and foraging tactics and along with sperm whales for their vocal repertoires (dialects) in the wild. Regarding their idiosyncratic foraging tactics, examples include intentional beaching (Guinet 1991; Guinet and Bouvier 1995; Lopez and Lopez 1985), the "carousel feeding" technique (Similä and Ugarte 1993), or the "cooperative wave- washing behaviour" to take seals off the ice floe (Pitman and Durban 2012; Smith et al. 1981) among others. As for their vocal dialects matrilineal units or pods within a population have been documented to deploy a combination of unique and shared call types (Deecke et al. 2000; Ford 1991; Miller and Bain 2000). All these motor and vocal behaviors are believed to be transmitted via social learning, not only from mother to offspring (vertical transmission), but also between matrilines (horizontal transmission) and do not correlate with geographical distance (Filatova et al. 2012), therefore, they do not seem to be either ecologically or genetically inherited and are often presented as model species of potential non-human cultural traditions (Rendell and Whitehead 2001). Supporting this observational evidence, we have already reported that orcas are capable of copying familiar and novel motor actions and sounds demonstrated by conspecifics and humans, with remarkably positive results in both modalities, that are comparable to

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

Novelty	Timing	Type	Species	References
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)
			Dolphin	Bauer and Johnson (1994); Jaakkola et al. (2010, 2013)
			Beluga	Abramson et al. (2017)
			Orca	Abramson et al. (2018)
	Deferred	Transitive	Great apes	Bering et al. (2000); Bjorklund et al. (2000, 2002); Bjorklund and Bering (2003); Yunger and Bjorklund (2004)
			Dog	Fugazza et al. (2016a, b); Fugazza and Miklosi (2014, 2015)
			Dolphin	Kuczaj and Yeater 2006) and Yeater and Kuczaj (2010) for reviews
		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	Huber et al. (2009)
		Intransitive		

that observed in dolphins tested under similar experimental conditions (Abramson et al. 2013, 2018). However, the question of how much flexibility and cortical control of this ability exists in this species and the presence of the capacity for deferred imitation of intransitive actions in delphinids remains open.

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

Our rationale is that if subjects are able to copy intransitive actions demonstrated by a conspecific after a delay interval, even when exposed to distractors during the retention interval, we may be able to rule out "delayed object enhancement" (Hoppitt and Laland 2008) and an "automatic and delayed" response facilitation effect, explained by alternative explanations such as that the subjects adopted a stereotyped posture or rehearsed mentally or motorically the target actions during the retention interval (Herman 2002). This would allow us to conclude that the orcas are "in control" of their matching response (since the subjects would only reproduce the action of the model that was indicated by the "copy" command). Conversely, if they would copy the last behavior performed by the demonstrator or the one performed by themselves (distractors), it would support the idea that the matching response was "automatically" triggered, which could be explained by a response facilitation effect.

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

Methods

(a) *Subjects*

We tested two orca (*Orcinus orca*) subjects, a 15-year-old male named Inouk, and a 20-year-old female named Wikie, both housed at Marineland Aquarium in Antibes, France. The conspecific models, Moana and Keijo, were their calves, two males, 5 and 2 years old, respectively. All subjects were born in the aquarium, were mother-reared, and lived together in a social group, with access to five differently sized pools. All subjects had been trained for a variety of examination and exercise behaviors with standard operant conditioning procedures and fish/tactile positive reinforcement. The subjects had participated in a previous action imitation study (Abramson et al. 2013), so they were already trained with the "copy" command. Experimental sessions were done between December 2017 and July 2021. During the experiments, subjects were tested in pairs in their pools and were not food deprived. Testing was interrupted if subjects were distracted or disinclined to participate.

(b) *Procedure*

Each testing session consisted of 1–3 blocks of 3 trials, lasting approximately 10–20 min altogether. There were 1–4 sessions per day. The first two first trials of the testing sessions were our "baseline" delay trials (delays of 5 and 15 s, respectively). These two baseline delays helped us to check if the subjects were motivated to participate in the session and paid attention to the model. If they failed in any one of them we canceled the session and did not present the "test delay trial" (this occurred only in one session with Inouk and in three sessions with Wikie). But if they succeeded, the test trial was presented and scored as correct or incorrect.

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

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

Table 3 Behaviors tested

Behavior	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 splah (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 behavior 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

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

Phase 1. Preliminary training for deferred imitation

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

Inouk succeeded in 100% of the trials (36/36) and Wikie in 88% of the trials (44/50) in their first four sessions; however, from the fifth session onwards their performance began to decrease, sometimes failing even in the 5-s baseline delay trials that they had mastered previously. We concluded that this drop in performance might be caused by the long duration of the sessions, which negatively affected their attention and motivation. Therefore, we decided to shorten the duration of the sessions and changed the configuration of the trial presentations to one up to four short blocks interspersed by 5-min (or longer) breaks. From the 15th session onwards, the subjects went through the training sessions with this new protocol of each block consisting of three trials of different behaviors with interval delays of 5, 15 and 30 s, respectively. When subjects reached a criterion of more than 80% correct responses to 30-s delay trials in two consecutive sessions, they advanced to phase 2.

Phase 2: deferred imitation (with no distraction) testing procedure

This condition was tested with one of the two subjects, Inouk. Testing sessions followed the same configuration as the last training sessions consisting of one up to three blocks of three trials in which the two first trials were “baseline” delay trials (with delays of 5 and 15 s, respectively). These two baseline delays helped us to check if the subjects were motivated to participate in the session and paid attention to the model. Then, we finished the block with a “test delay trial” in which the retention intervals were gradually increasing from 60 to 90, 120 and 150 s over successive sessions. Six trials of deferred imitation of different behaviors chosen randomly without replacement from the list of nine familiar behaviors were run for each one of these retention intervals (see Tables 3 and 4). Only one trial of the longest delay interval was presented within any block in any given session throughout the procedure.

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

	Inouk	Wikie
Phase 2: no distraction		
Delay		
45	100	
60	100	
90	100	
120	100	
150	83	
Phase 3a: model distracting		
Delay		
45	100	
60	100	
90	83	
120	100	
Phase 3b: observer distracting		
Delay		
45		83
60		100
90		83
120		100
150		67

Control trials for behavior specific cues ("Clever Hans" control)

After the completion of the variable delay testing procedure, four control trials were run to ensure that the subjects' correct responses were not based on some procedural or behavioral artifact that cued the identity of the demonstrated behavior after the completion of the delay interval. Prior to each trial during the control sessions, the T_S closed his eyes and turned his body away from the demonstrator, to prevent him from seeing the model's behavior. At the end of the variable delay interval, the experimenter verbally cued the T_S to give the copy command to the subject. After Inouk's response, the T_S was cued by the experimenter to either reinforce him for a correct response or prepare him for the next trial. Six control sessions were run, using the same set of four delays—baseline delays after 5 s, 15 s, and the longest delay tested, 150 s.

Phase 3a: deferred imitation with distraction (model distracting) testing procedure

This phase was run with Inouk, the subject tested in phase 2. In this condition, the subject observed the demonstration of the target action and was then distracted during the retention interval by asking the demonstrator to perform a non-target action that the subject was not requested to copy. The non-target actions were the same actions used in the Do as I Do training and testing extracted randomly from the list (Table 3). The subject was then requested to continue waiting in the starting position until he received the "copy" command to perform the target action. We began with two training sessions with 30-s distraction trials as the longest delay. Testing involved the subject's response to the T_S's copy command with the same variable delay intervals tested in the previous phases (from 45 to 60, 90, 120 and 150 s over successive sessions), but now, with the potential interference of the non-target action that the model also performed during the retention time.

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

Phase 3b: deferred imitation with distraction (observer distracting) testing procedure

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

(c) *Coding and data analysis*

Coding was done mainly by one experimenter, who watched the videos of each test trial and recorded whether the subject's action was a correct match of the demonstrator's action. For reliability analysis, a second experimenter coded 30% of the trials, watching just the subject's actions but not the trainer's signal. Interobserver reliability was perfect (Cohen's kappa coefficient for the observed behaviors was 1, $p < 0.001$). Exact binomial tests for each phase and delay interval were performed to investigate whether the individuals successfully copied the demonstrator's actions above chance. To estimate the probability of copying by chance, we adopt a rather conservative criterion, assuming that chance performance for each subject in each trial would be 0.10, that results from 1/[*number of different behavior requested to be performed* + 1 (*possibility of doing nothing*)]. Note that this criterion is very conservative, given that in theory, the subject had the possibility to select and perform any other action from their repertoire requested usually as part of their training exercises, rather than just those, namely, the target actions, requested in the test situation.

Results

Phase 1 training

The two subjects recalled the copy command ("Copy this!") given by the trainer that they had last used up to seven years earlier as indicated by their response in the first trial. Both subjects started copying the demonstrator's actions after the baseline delays (of 3, 5 and 15 s) from the very beginning of testing. The criterion required to reach correct performance, that is, 80% in two consecutive sessions of 30-s delay trials (that is, excluding the baseline delays of 3, 5 and 15 s in which both subjects were over 95% correct performance), was achieved by both subjects after 11 30-s trials (see Table 4).

Phase 2: deferred imitation (with no distraction) testing procedure

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

Control trials for behavior specific cues ("Clever Hans" control)

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

Phase 3a: deferred imitation with distraction (model distracting) testing procedure

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

Phase 3b: deferred imitation with distraction (observer distracting) testing procedure

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

Discussion

The two orcas participating in the present experimental study of social learning recalled in the first trial the copy command ("Copy this!"), which they had last used up to 7 years earlier, and reproduced intransitive (body-oriented) actions demonstrated by a conspecific after delay intervals of up to 150 s. Their *deferred* matching performance was successful even when the subjects were exposed to two types of *distractors* during the retention interval. Remarkably, their performance was hampered neither by watching other non-target actions demonstrated by the model nor by non-target actions that the subjects were asked to perform themselves during the retention interval. Their successful performance in these cognitively challenging conditions rules out alternative explanations such as that the subjects adopted a stereotyped posture or rehearsed mentally or motorically the target actions during the retention interval (Herman 2002). It further indicates that the orcas' matching ability was flexible and selective, two alleged signatures of cognitively complex social learning (Hoppitt and Laland 2008; Huber et al. 2009).

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

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

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

Previous comparative work on deferred imitation has mostly focused on the copying of *transitive*, object-oriented, actions (great apes: Bering et al. 2000; Bjorklund et al. 2000; Bjorklund et al. 2002; Bjorklund and Bering 2003; Tomasello et al. 1993; Yunger and Bjorklund 2004; dogs: Fugazza et al. 2016a, 2016b; Fugazza and Miklosi 2014, 2015; see Table 2). It is generally agreed that copying transitive actions is less cognitively demanding than imitating intransitive actions (Heyes and Ray 2000; Subiaul 2007, 2010; Zentall 2003, 2011). Indeed, in the latter, the subject must copy the body movements without any object in the environment that helps to "enhance" the memory or guide the action to be displayed (Tennie et al 2009). In contrast, Herman's study (2002) of deferred imitation in dolphins and the present work of deferred imitation in the orca involved intransitive, body-oriented, actions. The difficulty of reproducing intransitive actions is further increased when a delay is introduced between observation and reproduction. Therefore, the present study's results on deferred imitation of intransitive actions provide remarkably solid evidence to rule out "delayed object enhancement" (Hoppitt and Laland 2008) and automatic response facilitation in a non-human animal, as: (a) no environmental cue was present (other than the action of the demonstrator itself), (b) two types of control conditions were introduced (i.e., the demonstrator and the observer performed non-target, distractor actions during the retention interval) and (c) the success rate of matching did not decline significantly, not even at delays almost twice as long as the longest delay tested by Xitco (1988) in the bottlenose dolphin.

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

Studies of immediate and deferred imitation of several species of cetaceans, including bottlenose dolphins (Herman 2002; Xitco 1988), belugas (Abramson et al. 2017), and orcas (Abramson et al. 2013, 2018, this study) have all highlighted their propensity to engage in actions requiring high levels of interindividual behavioral synchrony and coordination in several contexts, particularly during hunting (Lopez and Lopez 1985; Pitman and Durban 2012; Visser et al. 2008). Orcas are large-brained, socially complex, and highly cooperative water-dwelling mammals (Marino 2022). They have also been reported to possess group-specific behavioral traditions and vocal dialects hypothesized to be socially learned (Filatova et al. 2015). Several researchers have highlighted the notably conservative nature of the orcas' traditions or "cultures", where innovation is typically infrequent, but can spread very fast once it emerges (Barrett-Lennard and Heise 2007; Whitehead and Rendell 2014). This strong proclivity to copy what others are doing and to conform to the actions of their group members may be a key driver of intergroup differentiation and intra-group identity (Byrne 2009; Meltzoff and Decety 2003), ultimately resulting in the reproductive isolation of sympatric groups and incipient speciation (Riesch et al. 2012).

Conclusion

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

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

Taken together, the findings from this experimental study suggest that the orcas may have the potentiality to control from whom, what and when matching others' actions. This capacity of orcas to copy under voluntary control what others are doing would be consistent with the body of observations on group-specific behavioral traditions and vocal dialects, synchronized behavior, and sophisticated cooperative strategies and could be at the base of the conformity to the group's normative traditions, documented in this species (Barrett-Lennard and Heise 2007; Lopez and Lopez 1985; Filatova et al. 2015; Pitman and Durban 2012; Visser et al. 2008; Whitehead and Rendell 2014).

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Code availability No code was used in relation to this paper.

Declarations

Conflict of interest The authors declared that they had no conflicts of interest with respect to their authorship and/or the publication of this article.

Ethical approval The Laboratory Animal Care and Use Committee (CICUAL) of the School of Medicine, Universidad del Desarrollo of Chile (UDD), have approved this research. This research adhered to the legal requirements of the country (France) in which the work was carried out and Marineland institutional guidelines.

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