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Experimental evidence for action imitation in killer whales (*Orcinus orca*)

José Z. Abramson · Victoria Hernández-Lloreda · Josep Call · Fernando Colmenares

Abstract Comparative experimental studies of imitative learning have focused mainly on primates and birds. However, cetaceans are promising candidates to display imitative learning as they have evolved in socioecological settings that have selected for large brains, complex sociality, and coordinated predatory tactics. Here we tested imitative learning in killer whales, *Orcinus orca*. We used a 'do-as-other-does' paradigm in which 3 subjects witnessed a conspecific demonstrator's performance that included 15 familiar and 4 novel behaviours. The three subjects (1) learned the copy command signal 'Do that' very quickly, that is, 20 trials on average; (2) copied 100 % of the demonstrator's familiar and novel actions; (3) achieved full matches in the first attempt for 8–13 familiar behaviours (out of 15) and for the 2 novel behaviours (out of 2) in one subject; and (4) took no longer than 8 trials to accurately copy any familiar behaviour, and no longer than 16 trials to copy any novel behaviour. This study provides experimental evidence for body imitation, including production imitation, in killer whales that is comparable to that observed in dolphins tested under similar conditions. These findings suggest that imitative learning may underpin some of the group-specific traditions reported in killer whales in the field.

Keywords Social learning · Imitation · 'Do-as-other-does' test · Animal culture · Killer whales

J. Z. Abramson (✉) · F. Colmenares
Grupo UCM de Estudio del Comportamiento Animal y Humano,
Departamento de Psicobiología, Facultad de Psicología,
Universidad Complutense de Madrid, Madrid, Spain
e-mail: zabramson@psi.ucm.es

V. Hernández-Lloreda
Grupo UCM de Estudio del Comportamiento Animal y Humano,
Departamento de Metodología de las Ciencias del
Comportamiento, Facultad de Psicología,
Universidad Complutense de Madrid, Madrid, Spain

J. Call
Department of Developmental and Comparative Psychology,
Max-Plank Institute for Evolutionary Anthropology,
Leipzig, Germany

Introduction

Learning to do things the way others do them rather than learning solely from one's individual experience is considered one of the most important adaptive benefits of sociality and one of the key drivers of the evolution and development of culture (e.g. Gergely and Csibra 2006; Laland and Galef 2009; Meltzoff and Decety 2003; Tomasello 1999). The comparative study of social learning and imitation has generated considerable debate in the behavioural sciences (Bates and Byrne 2010; Caldwell and Whiten 2002; Laland and Galef 2009). In fact, imitation along with teaching has been claimed to be key defining characteristics of what makes human culture unique in the animal kingdom (Tomasello 2009). The faithful reproduction of a demonstrator's behaviour via imitation, often considered a hallmark of human cultural traditions, not only produces within-group uniformity at a particular point in time but also enables the accumulation of modifications over time (i.e. the ratchet effect) (Tomasello 2009).

The most convincing demonstration of imitation involves the copying of another's action in the absence of any other scaffolding information (e.g. copying of results

or copying the consequence of an action). If the behaviour copied by the 'observer' from the 'demonstrator' is novel, that is, does not pre-exist in the observer's behavioural repertoire, the term production imitation is often used (Byrne and Russon 1998; Byrne 2002). This kind of imitation, also referred to as 'complex imitation' (Heyes 2012), 'imitative learning' (Tomasello 1996), or 'true imitation' (Zentall 2006), is thought to reflect the operation of complex cognitive processes (see Zentall 2006), and to bring about important functional consequences, including the non-genetic transmission of potentially fitness-enhancing information that may drive intergroup differentiation and intragroup transmission of local traditions.

Although there is a considerable body of work on imitation in birds, most studies on mammalian imitation have focused on great ape species and, recently, on dogs as well (see Huber et al. 2009; Zentall 2006 for reviews). However, there are other mammalian species that should theoretically be expected to evolve some of these social learning skills, as they exploit socioecological niches that have selected for some convergent adaptations such as large brains, long juvenile periods, complex sociality, and coordinated hunting tactics. Cetaceans are clearly a case in point; in fact, dolphins are often mentioned in reviews of imitation research as holding promise for the possession of cognitive skills comparable to those of great apes (Herman 2002; Marino 2002; Yeater and Kuczaj 2010). Experimental evidence for the ability to imitate in cetaceans has been demonstrated only in the bottlenose dolphin, for vocal imitation (Richards et al. 1984; Richards 1986), and for action imitation (Bauer and Johnson 1994; Herman 2002; Xitco 1988). Specifically, in action imitation Xitco (1988) reported that two dolphins could be trained to imitate a human or another dolphin on command for familiar as well as for novel behaviours. Bauer and Johnson (1994) extended these results by training two naïve dolphins to imitate a set of familiar and two completely novel behaviours on command, although neither dolphin imitated the novel behaviours. In other studies, dolphins also showed the ability to copy behaviours presented to them via television (Herman et al. 1993) and to 'repeat' the last behaviour they themselves produced, which could potentially be seen as imitation of their own actions (Mercado et al. 1998). Finally, dolphins were able to perform a variety of unstructured new behaviours created by themselves together in close synchrony both in timing and in characteristics (Herman 2002, 2006), a performance that requires imitative skills and were also able to imitate the behaviors of another dolphin in a blindfolded (i.e. wearing eyecups) condition (Jaakkola et al. 2010).

Like dolphins, killer whales have relatively large brains, advanced social systems, and high trainability, which make them share many striking parallels with primates (Marino

et al. 2007; Yurk et al. 2002). However, unlike dolphins (and primates), killer whales' cognitive abilities are largely unknown. Killer whales are often presented as representative species of potential non-human cultural traditions with group-specific vocal repertoires and motor behaviours (Rendell and Whitehead 2001). Although the existence of social traditions does not prove imitative learning per se, there have been observational reports of specific behavioural tactics in killer whales, which suggest that imitative learning might be at work. Examples include the intentional beaching to capture sea lions that occur in the Crozet Islands and in Punta Norte, Argentina (Guinet 1991; Guinet and Bouvier 1995; Lopez and Lopez 1985), the rubbing on gravel at particular beaches (Bigg et al. 1990; Matkin et al. 1997), the 'greeting ceremony' observed in the Southern Residents (Osborne 1986), the 'carousel feeding' technique used by killer whales off Northern Norway to herd and prey on herring schools (Similä and Ugarte 1993), the benthic foraging on stingrays in shallow water of the North Island of New Zealand (Visser 1999), the endurance–exhaustion technique for capturing bluefin tuna in the Atlantic (Guinet et al. 2007), and the 'cooperative wave-washing behaviour' displayed by type B killer whales in the Antarctica to take seals off the ice floe (Smith et al. 1981; Pitman and Durban 2012). In the light of these observations, several researchers have suggested that the killer whales' calls, dietary preferences, and foraging behaviours have strong cultural components and have hypothesized that imitation is probably the main social learning mechanism involved (Barrett-Lennard and Heise 2007; Deecke et al. 2000; Ford 1991; Weiß et al. 2010; Yurk 2003). In contrast, other scholars have argued that the evidence for imitation in killer whales is weak at best and that their 'cultural traditions' can be explained by other less complex learning processes (Caro and Hauser 1992; Galef 2001). To elucidate the social learning mechanisms that underpin these 'cultural traditions', experimental studies are necessary.

The aim of this study is twofold. We investigated whether killer whales were capable of imitating on command the actions performed by a conspecific demonstrator. The 'do-as-other-does' method used in the current study offered us two major benefits. First, it allowed us to determine whether imitation (i.e. copying the demonstrator's action) rather than emulation (i.e. copying the results of the demonstrator's action) was at work, as the demonstrator's actions did not produce changes in the environment (Carpenter and Call 2009). This paradigm has been used with birds (Moore 1992), primates (Call 2001; Custance et al. 1995; Myowa-Yamakoshi and Matsuzawa 1999; Tomasello et al. 1993), dogs (Topal et al. 2006; Huber et al. 2009), and dolphins (Bauer and Johnson 1994; Herman 2002; Xitco 1988). Second, it allowed us to test

killer whales' capacity to imitate both familiar and novel actions (see below). By novel actions, we mean actions that have never been trained or displayed by the subjects (Whiten 2000). The latter kind of imitation, dubbed production imitation (e.g. Bates and Byrne 2010; Byrne 2002), is more cognitively demanding than the former because it entails an individual acquiring a new motor schema out of components in its pre-existing repertoire, just from watching a more expert demonstrator (Byrne 2002; Byrne and Russon 1998).

Methods

Subjects

We tested 3 killer whales, *Orcinus orca*, housed at Marineland Aquarium in Antibes, France: Val, a 13-year-old male; Inouk, a 10-year-old male; and Wikie, a 8-year-old female. 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 behaviours with standard operant conditioning procedures and fish/tactile positive reinforcement. During experiments, subjects were tested in pairs in their pools and were not food deprived. Testing was interrupted if subjects refused to participate.

Procedure

General procedure

Forty-eight experimental sessions were conducted. Each session consisted of 8–12 trials, lasting approximately 20–45 min altogether. There were 1–3 sessions per day, 6–7 days a week. Some sessions were terminated earlier if subjects were distracted or disinclined to participate (this occurred in just one session). To run the experiments two trainers were needed, one to give the signal to the demonstrator (T_D) and another to give the copy command to the subject (T_S). Subjects were positively rewarded with fish and with tactile and voice reinforcement signals whenever they yielded a correct response. They received no reinforcement following errors. Reinforcement of the demonstrator was not contingent upon the response of the subject. The study comprised three phases. *Phase 1* involved training the subjects to respond to the gesture-based command 'copy' ('Do that') given by the trainer. *Phase 2* involved testing the subjects' response to the trainer's copy command when the demonstrator performed familiar behaviours, that is, behaviours that the subjects had already seen others perform and had performed themselves. We

only report behaviours that were tested at least five times, unless the subject copied them earlier. Finally, in *Phase 3*, the subjects were tested with novel behaviours, that is, behaviours that were unknown to the subject in terms of neither having been exposed to them nor having been seen to be performed by him/her previously. Behaviours performed by demonstrators were grouped into three categories: (a) familiar behaviours that were used when the subjects were being trained to respond to the copy command given by the trainer (Phase 1) and subsequently, during the testing sessions, when the subjects had already learned to respond to the trainer's copy command and were requested to do what the demonstrator was doing (Phase 2); (b) familiar behaviours that were used during the testing sessions (Phases 2 and 3), but not during the training sessions (Phase 1); and (c) novel behaviours (Phase 3), learned by one of the subjects (the demonstrator) and unknown to the others (each killer whale was tested with two novel behaviours). Table 1 gives the complete list of behaviours examined in this study, and Table 2 gives a summary of the behaviours used in each phase by subject. All familiar behaviours used in this study were not part of the killer whales' natural repertoire but the result of the trained set of actions that subjects regularly were requested to perform during the aquarium shows and veterinary examinations. All sessions were videotaped by two video cameras located across and above the tank in a position that provided a full view of the two subject–trainer pairs and the entire tank.

Phase 1: training sessions

The design of the training sessions was inspired by a previous 'squirt game' that one of the trainers used to perform with two of the study subjects. The game can be described as follows. While the two whales were located in adjacent pools, the trainer gave the 'squirt signal' to the two subjects, so that both were required to do the action in tandem, and they responded by squirting each another. Then, we took advantage of this set-up and expanded it. Thus, we requested these two subjects to do the same thing, but now with another familiar behaviour that had never been requested in this new context. This time the signal was directed to one of the subjects (Val) and was relatively hidden from the other (Wikie). As soon as the demonstrator started to perform the behaviour, the trainer directed her sight to the subject, looking at her and directing her attention by pointing at the demonstrator. Surprisingly, the subject reproduced the demonstrator's action, generalizing the 'game' in a single trial. Nevertheless, it is important to note that, at this stage, the subject could see the signal that the trainer gave to the demonstrator, even though it was not directed at her (see the online resource ESM_1.mpg; video captions can be found in the online resource ESM_7.pdf).

Table 1 Behaviours tested in each phase

	Description
Familiar behaviours	
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 wave (PW)	Turn on one side, one pectoral fin out of the water, and wave it back and forth out of the surface
Pec mimic (PM)	Pectoral fin out of water while keeping it motionless a few seconds
Pec splah (PS)	Pectoral fin out of water while keeping it motionless a few seconds and then slap once and heavily on the water
Spy hop (SH)	Turn 180°, back to the trainer, rise vertically on water with half of the body outside the surface
Fluke present (FP)	Roll 180° to ventral up position, turn 180° to head tail position, take the tail out of the water next to trainer position
Tongue out (TO)	With the head out of the water take out (showing) the tongue
No (NO)	Shake head back and forth from left to right
Yes (YES)	Nods head down up and down
Posse (PO)	Take half of the body out of the water while keeping posse with the pectoral fins and the chest in the border of the pool for one to two seconds
Fluke wave (FW)	Dive downward to a vertical position with tail fluke protruding from the water and shaking it
Novel behaviours	
Inverse tapec caudal (ITC):	Turn over, ventral side up with the head towards the middle of the pool and the tail towards the starting point (head tail position), and make one big tail splash with tail fluke protruding highly out of the water
Barric roll static (BRS)	Lie in a horizontal position and turn over and over while remaining in the same place
Airplane (AIR)	Turn on one side lifting one pectoral fin out of the water first and then the same with the other side. Alternate this action in a continuous and vigorous motion
Bottom resting (BR)	Dive to the bottom of the pool with entire body disappearing underwater in downward motion and then keep the whole body resting in a horizontal position in the bottom floor of the pool for about 10–40 s

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

From here onwards, the two individuals, demonstrator and subject, faced each other in two contiguous pools separated by a corridor (1.5 m wide approximately), where the trainers (T_D and T_S) stood back to back facing the demonstrator and the subject, respectively. The demonstrator was first required to perform a randomly selected familiar behaviour by T_D. When the demonstrator performed the required action, T_S directed the subject's attention to the demonstrator by pointing at her/him and introduced the command copy (a visible gesture made up for this purpose). This sequence was repeated until the subject produced an action. Unexpectedly, as every tested subject copied the demonstrator's behaviours in 70 % of the trials (the correct criterion performance set to go to the test phase) from the very beginning, individuals received just one to two training sessions with a total of 10–37 trials depending on the subject. Since the subjects copied the demonstrator's actions from the very beginning, we decided to introduce four to six different actions (as shown in Table 2) in this training phase, instead of just one or two, in order to prevent the animal from learning the copy action

as an alternative second signal for previously known behaviours. (The reason for doing this was because trainers sometimes used two different signals for the same action.)

Testing sessions: general procedure

Throughout all testing sessions, both trainers were positioned at different sides of a white wooden panel of 2 m × 1 m placed in an oblique position in such a way that the subject and the demonstrator could see each other and their trainer, but could not see the other trainer's signal. T_D was positioned to the left side of the panel, and T_S was at the right side; thus, the trainers were in a position from which they were not able to see each other's signals and were cued individually by the experimenters for the conditions in which they could not see the demonstrator's behaviour and could not, therefore, assess whether his or her subject had copied or not correctly. Two different set-ups were used, with this same panel/trainer configuration in each pool: *two different pools* (Set-up 1) and *one pool* (Set-up 2) (Fig. 1). Set-up 1 (*two pools*) was the set-up that had

Table 2 Behaviours and number of trials by subject and study phase

Behaviour	Number of trials		
	INOUK	VAL	WIKIE
Training			
FW		5	3
HU	3	5	
PW	1	8	5
RO		5	
SO	1	4	1
SQ		4	3
TC	1	6	
Test: familiar behaviour			
FP		3	2
FW	11	12	16
HU	15	14	11
NO	13	5	4
PM	4	3	2
PO	9	4	2
PS	5	3	1
PW	10	10	9
RO	15	7	4
SH	3	14	6
SO	23	14	12
SQ	11	7	9
TC	21	13	11
TO	2	5	2
Yes	8	11	2
Test: novel behaviours			
AIR	10		4
BRS		6	5
ITC		16	
BR	19		

been used in the training trials, with the exception that, in this case, the opaque panel was placed between the two trainers. This set-up served as a control condition to rule out the possibility that a trainer who saw the demonstrator's behaviour could cue in some way the subject. It served, as well, as a transition set-up from training to the test sessions that later were carried out in the same pool (the arrangement in the training sessions was the same as in the testing conditions). The use of the same pool set-up (Set-up 2) was necessary as some of the demonstrator's behaviours were difficult for the subject to see when both whales were placed in two different pools (see the online resource ESM_2.mpg). Nevertheless, given the nature of the behaviours performed and the kind of signals that trainers used to request them, potential trainer cues are not a realistic alternative explanation. Set-up 1 was also used

when particular conditions at the aquarium (or animal's circumstances) prevented us from keeping the two individuals in the same pool. In Set-up 2 (*one pool*), the subjects were placed in the same pool, one next to the other. The demonstrator was positioned to the left of the subject (for an example, see Fig. 2b and the online resource ESM_2.mpg; video captions can be found in the online resource ESM_7.pdf).

Phase 2: testing familiar behaviours

The acquisition of the actions used in the training sessions and the generalization to other behaviours of the subjects' repertoire of actions was tested. Thus, new familiar behaviours shared by all subjects plus the familiar behaviours already used in the training phase were tested. Sessions consisted of one to two control trials and 6–12 test trials. Behaviours were presented with the constraint that no more than three test trials of the same familiar behaviour could occur in a row. In Set-up 1, an observer judged the correctness of each trial and told the trainers to reinforce or not the subject. After a couple of sessions, we used the same protocol as in Phase 1, but we changed the pool configuration to Set-up 2, so that the subject could have a better view of the details of the model's body movements. Fifteen actions were presented in this phase, resulting in more than 100 trials altogether for each subject (Table 2). The number of trials per familiar behaviour presented to each subject varied during the study (see Table 2) for different reasons. First, our goal was to determine whether they were able to copy at all and how long they took to succeed rather than if their matching skills were behaviour specific. It is important to note that all the familiar behaviours used were actions previously trained, and in this regard, we assumed that they were equally difficult to copy. Therefore, in our experimental paradigm, running a similar number of trials for each behaviour was not required. Second, since subjects varied in the number of trials they required to reach the performance criterion in each of the novel behaviours, we adjusted the number of test trials per individual and per behaviour accordingly. Lastly, there were also other practical considerations having to do with animal and facility management (e.g. the testing pool was not the same throughout the study) that influenced the number of trials. Finally, our calculations for familiar behaviours also included those exemplars that were interspersed with the novel behaviours during Phase 3. Trials of the familiar behaviour FP that were tested in Set-up 1 (opposite pools) were excluded from the analyses because we found that subjects had great difficulty seeing the demonstrator's behaviour in that set-up.

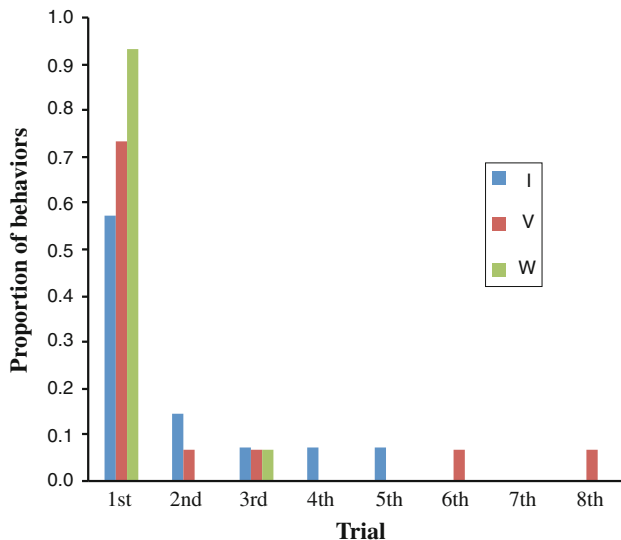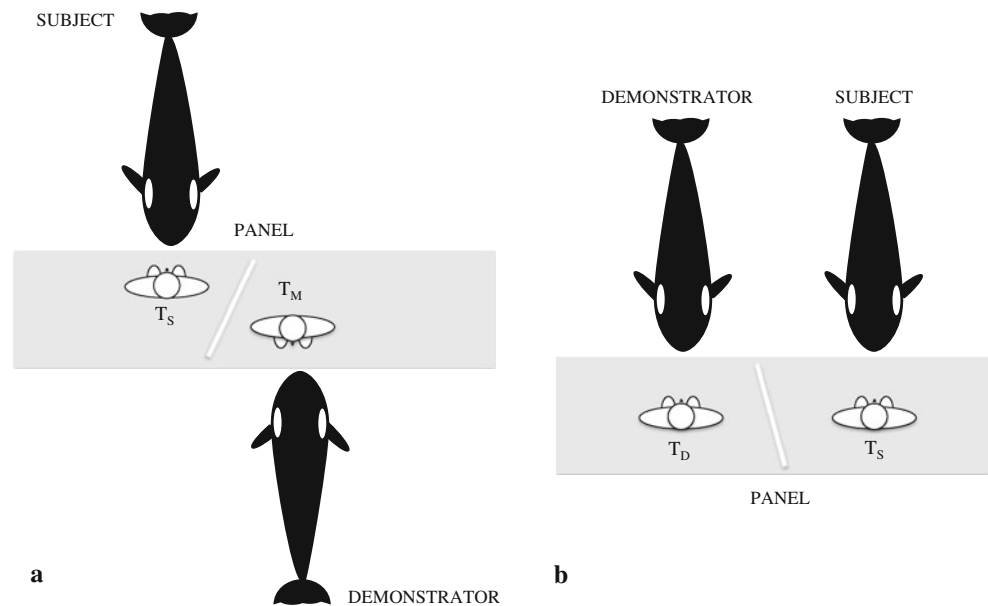**Fig. 1** Experimental set-up:
a set-up 1; **b** set-up 2

Fig. 2 Number of trials to achieve a 'full reproduction' action in familiar behaviour testing

Phase 3: testing novel behaviours

We used the same protocol as in Phases 1 and 2, but in this case we introduced, along with familiar behaviours and control trials, a novel or untrained behaviour that had been previously taught to only one subject, the demonstrator, but was completely unknown to the others. Four different novel behaviours were trained and later tested. Inouk was trained to perform *Barric Roll Static* (BRS); Val was trained to perform *Airplane* (AIR) and *Bottom Rest* (BR); and Wikie was trained to *Inverse Tapec Caudal* (ITC) (Table 1). In each session, a single novel behaviour was presented to each subject at a time. We also interspersed

familiar behaviours that had been used in the previous phases. Within each block of 5–12 trials, up to five trials of the novel behaviour were presented, with no more than three consecutive twice in a row. The subject received both fish and social and tactile reinforcement only for an accurate matching. Neither the demonstrator nor the subject received reinforcement for incorrect responses, or for partial matches (familiar behaviours similar to the untrained behaviours) or for reproducing only some aspect/ components of the novel behaviour.

Data coding and analysis

Coding was done by the experimenters, neither of whom had been present during the training sessions. Coder 1 coded the videos several hours after the testing sessions, and coder 2 coded several months after the study has been completed. One experimenter (coder 1) 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 (coder 2) watched 30 % of the trials. This second coder could see the subject's actions but could not see the trainer's signal. Interobserver reliability was excellent (Cohen's kappa coefficient for the observed behaviours was 0.97 and for the goodness of the performance was 0.95, all $ps > 0.001$). We used exact binomial tests to investigate whether the individuals successfully copied the demonstrator's actions above chance. For the analyses of the familiar behaviours, we assumed that chance performance for each subject would be success on 1/[*number of different familiar behaviour requested to be performed* + 1 (possibility of doing nothing)] trials. We assumed a chance performance

for Inouk and Wikie equals to 1/14, and for Val equals to 1/15. Note that this is a rather conservative criterion, given that in theory, the subject had the possibility to perform any other action from the repertoire of behaviours taught by the trainers and requested usually as part of their training exercises, rather than just those requested in the test situation. For the analysis of the untrained actions, we assumed that chance performance would be success on 1/[*number of different familiar behaviour requested to be performed* + 2 novel behaviour + 1 (possibility of doing nothing)] trials. Note that this is even more conservative, given the fact that theoretically the subject had the possibility to perform any other action rather than the untrained behaviours. Šidák adjustments for multiple exact binomial tests performed for each subject (a total of 14 for Inouk, 15 for Wikie, and 16 for Val) were used to achieve a family-wise alpha of 0.05 for each subject. Since every behaviour was not tested the same number of trials, another criterion to test whether individuals performed above chance for a particular behaviour is to consider as the probability test the actual proportion of times that any particular behaviour had been tested. We analysed the data using this criterion as well, but it did not change the results.

For familiar behaviours, following Call (2001), we judged the level of matching accuracy of each attempt using the following three-point scale: (1) full reproduction (1), the behaviour was reproduced in its entirety; (2) partial reproduction (0.5), when some elements of the modelled action, such as the body parts involved, or the orientation of the actions was missing (or, for instance, doing PW, when PM is required [the pectoral fin should remain in static motion]); and (3) failed reproduction (0), the subject performed an action that was completely unrelated to the one performed by the demonstrator. For assessing novel behaviours, we used a four-point scale that added the category 'almost full reproduction' (0.75) to the other three. This finer-grain scale allowed us to further identify minor differences in the level of behavioural matching (e.g. exact body orientation/rhythm) between the demonstrator's performance and the subject's reproduction.

Results

Training

The three subjects started copying the demonstrator's actions from the very beginning (see video in the online resources ESM_1.mpg). The criterion required to reach correct performance, that is, 70 % of trials, was achieved by Wikie in just 12 trials (two sessions), by Val in 37 trials (4 sessions), and by Inouk in 11 trials (two sessions).

Familiar behaviours

All three subjects copied 100 % of the demonstrator's behaviours. All behaviours were fully copied before the 8th trial, and many actions were copied in the first trial: Inouk copied 8 out of 14 (57 %) in the first trial; Val, 10 out of 14 (71 %); and Wikie, 13 out of 14 (93 %). The three subjects' performance was 100 % correct in control trials (when subjects were asked to perform a different action from the one performed by the demonstrator). Figure 2 shows the number of trials that subjects took to achieve full matching for familiar behaviours, Table 3 shows the percentage of trials in which the subjects performed a fully copied action of each familiar behaviour, and Table 4 shows the number of trials that subjects took to produce a full copy of the action, for each of the familiar behaviours. The three subjects performed remarkably above chance in the whole study: Inouk produced full matches for 83 % of the demonstrated actions, Val, 81 %; and Wikie, 94 % (all binomial tests: $ps < 0.001$). Analysing the actions separately, Wikie performed significantly above chance in 10 out of 14 behaviours (exact binomial tests with Šidák adjustments, $ps < 0.05$ for all actions) and, although not strictly statistically significant, copied 2 out of 2 trials (100 %) presented for each of the other 4 behaviours (binomial tests, $ps = 0.053$ with Šidák adjustments; note that Šidák correction resulted in a test-wise alpha of $p < 0.0032$ for Wikie and with just two trials, it is not possible to reach this criterion), Val in all but PO and RO, and Inouk in all but PO and TO (all $ps < 0.004$) (see Table 3 for a description of overall performance for each action per individual).

Novel behaviours

All three subjects copied correctly 100 % of untrained behaviours. All behaviours were fully copied before the 16th trial, and two novel actions were copied in the very first trial (see Table 5 for further details). Considering all the trials with novel behaviours, Inouk copied 41 % of the actions (binomial test: $p < 0.001$, $N = 29$), Val copied 57 % of the actions (binomial test: $p < 0.001$, $N = 21$), and Wikie copied 100 % of the actions (binomial test: $p < 0.001$, $N = 15$). It is important to note that for a copy to be considered a full match we adopted a rather strict criterion, individuals had to perform the same exact string of motor actions as well as the position and place in the pool where the actions were performed (for an example see online resource ESM_5.mpg). However, a closer look at the first attempts revealed that even in the trials in which their responses were incorrect, almost all subjects' actions appeared to be somehow influenced by the

Table 3 Overall performance (percentage of correctly copied actions) with familiar behaviours (including familiar trials tested in the novel behaviours test phase)

Behaviour	% p value, n					
	INOUK		VAL		WIKIE	
FP			67	$p = 0.15, n = 3$	**100**	$p = 0.053, n = 2$
FW	**64**	$p < 0.001, n = 11$	**83**	$p < 0.001, n = 12$	**100**	$p < 0.001, n = 16$
HU	**93**	$p < 0.001, n = 15$	**93**	$p < 0.00, n = 15$	**100**	$p < 0.001, n = 11$
NO	**62**	$p < 0.001, n = 13$	**100**	$p < 0.001, n = 5$	**100**	$p < 0.001, n = 4$
PM	**100**	$p < 0.001, n = 4$	**67**	$p = 0.01, n = 3$	**100**	$p = 0.053, n = 2$
PO	22	$p = 0.82, n = 9$	**60**	$p = 0.029, n = 5$	**100**	$p = 0.053, n = 2$
PS	**100**	$p < 0.001, n = 5$	**100**	$p = 0.035, n = 3$	**100**	$n = 1$
PW	**100**	$p < 0.001, n = 10$	**90**	$p < 0.001, n = 10$	**100**	$p < 0.001, n = 9$
RO	**93**	$p < 0.001, n = 15$	14	$p = 0.99, n = 7$	**100**	$p < 0.001, n = 4$
SH	**100**	$p = 0.004, n = 3$	**43**	$p = 0.001, n = 14$	**67**	$p = 0.003, n = 6$
SO	**91**	$p < 0.001, n = 23$	**100**	$p < 0.001, n = 14$	**100**	$p < 0.001, n = 12$
SQ	**100**	$p < 0.001, n = 11$	**100**	$p < 0.001, n = 7$	**100**	$p < 0.001, n = 9$
TC	**86**	$p < 0.001, n = 21$	**100**	$p < 0.001, n = 13$	**91**	$p < 0.001, n = 11$
TO	0	$n = 2$	**100**	$p < 0.001, n = 5$	**100**	$p = 0.053, n = 2$
Yes	**90**	$p < 0.001, n = 8$	**73**	$p < 0.001, n = 11$	**100**	$p = 0.053, n = 2$

Bold values represent statistically significant results ($p < 0.05$)

Exact binomial tests with Sidack correction

Table 4 Number of trials to reach a full copy of the action, for each familiar behaviour

Behaviour	Number of trials		
	INOUK	VAL	WIKIE
Test			
FP		3rd	1st
FW	5th	2nd	1st
HU	1st	1st	1st
NO	4th	1st	1st
PM	1st	1st	1st
PO	2nd	1st	1st
PS	1st	1st	1st
PW	1st	1st	1st
RO	3rd	8th	1st
SH	1st	6th	3rd
SO	2nd	1st	1st
SQ	1st	1st	1st
TC	1st	1st	1st
TO	*	1st	1st
Yes	1st	1st	1st

* It was just presented twice and the subject did not copy

demonstrator (as shown in online resources ESM_3.mpg and ESM_4.mpg). Figure 3 shows the subjects' performance in each trial, for each untrained behaviour analysed.
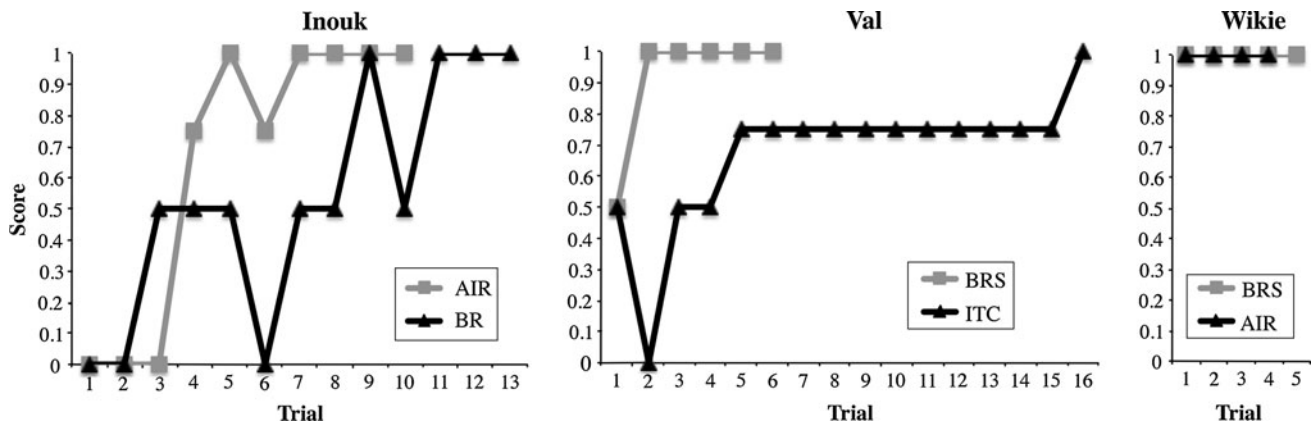
Discussion

This study produced experimental evidence for action imitation in the killer whale, a close relative of dolphins, the cetacean species that has received most research attention in this area (e.g. Herman 2010; Marino 2004). In the current study, killer whales learned to use the trainer's copy command quite quickly. In particular, they started responding to the trainer command after 20 trials on average (range, 11–37) and produced full matches of their conspecifics' behaviour no later than the 8th and 15th attempt for familiar and novel behaviours, respectively. As a matter of fact, an average of 71 % familiar actions (range, 53–87 %) and 50 % (2 out of 4) untrained actions were copied in the very first trial (see Tables 4, 5). Moreover, the three subjects copied 100 % of the demonstrator's familiar and novel actions tested ($n = 15$ and 4, respectively). One of the subjects performed above chance for all 15 familiar behaviours, and the other two subjects performed above chance for 14. As for the 4 novel behaviours tested, the three subjects performed above chance for all four.

The short training period that killer whales required to learn the copy command compares quite favourably with that observed in great apes and even dolphins. Thus, apes took from 3 months (Custance et al. 1995), to 8 months (Myowa-Yamakoshi and Matsuzawa 1999), and up to 9 months (Carrasco et al. 2009); naïve dolphins took from hundreds to 1,000 trials (Bauer and Johnson 1994); and

Table 5 Number of trials for each novel behaviour tested, trial number in which the demonstrator's action was fully copied, and number of trials in which each behaviour was fully copied after first full matching

Behaviour	INOUK			VAL			WIKIE		
	No. of trials	First trial	% correct after 1st copy	No. of trials	First trial	% correct after 1st copy	No. of trials	First trial	% correct after 1st copy
AIR	10	5th	80				4	1st	100
BRS				6	2nd	100	5	1st	100
ITC				16	16th				
BR	13	9th	80						

Fig. 3 Individual performance, by trial, in the copy of the new behaviours. Scores: 1 (full reproduction); 0.75 (almost full reproduction); 0.5 (partial reproduction); and 0 (failed reproduction)

dolphins, previously trained in tandem exercises, took from 17 to 26 training sessions (Herman 2002; Xitco 1988). It is also worth noting that in this study, killer whales showed little difficulty associating the trainer's signal to their copying response and they generalized a single 'mimic' signal to several familiar and untrained actions (as shown in online resources ESM_1.mpg and Table 2).

With respect to the familiar actions, killer whales were equally skilful at fully matching simple (e.g. PS) and complex actions (e.g. TP). Similarly, killer whales were equally capable of fully reproducing simple (e.g. BRS and AIR) and more complex untrained actions (e.g. ITC or BR), even though it took them longer to fully match complex actions. On the few trials in which the killer whales made errors, most of them tended to reproduce the major components of the demonstration nonetheless (Fig. 3).

Results from this study of three killer whales matched and extended those from dolphins imitating untrained actions in a similar 'do-as-other-does' task. In one case, our killer whales outperformed the dolphins. In Xitco's experiment (1988), one dolphin mimicked two of three novel behaviours demonstrated by another dolphin, both on the second trial, and another dolphin mimicked one of three novel behaviours on the third trial (Herman 2002). Finally, in Bauer and Johnson's study (1994), two dolphins did not

imitate novel behaviours, whereas the three killer whales of this study copied successfully all untrained actions they were presented with; in fact, one of them achieved full matching in the first attempt for both novel behaviours presented.

Experimental studies have shown that imitating others' actions on command is a difficult skill to train (Carpenter and Call 2009) since this ability requires the animal to understand the concept of imitation (Whiten 2000). It has been reported that enculturated apes, that is, individuals raised or trained by humans, are much better at imitating following demonstrations of actions than naive apes (see Call and Tomasello 1996). As it has been argued for enculturated apes, it is conceivable that the fast and accurate behavioural matching observed in the present study was due to their long and continuing history of training to respond to human commands. In fact, Bauer and Johnson (1994) suggested that the failure of the dolphins they studied to imitate might well be because they were undertrained. Nevertheless, the differences in the speed to learn to respond to copy commands in 'do-as-other-does' tasks between killer whales, dolphins, and great apes still remain (Herman 2002; Xitco 1988).

Taken together, these results suggest that killer whales may be particularly skilled in matching others' actions. A

case can be made that delphinids possess a natural capacity and propensity to imitate conspecifics' actions, the expression of which can be primed and enhanced under certain conditions, for example, when they are involved in naturally occurring social interactions, when they are exposed to ecological demands that require highly synchronous and coordinated group activities such as hunting, or when they participate in training sessions in a captive setting (see Baird 2000; Herman 2010; Pitman and Durban 2012; Yeater and Kuczaj 2010). Although behavioural synchrony can be achieved by other cognitive mechanisms such as response facilitation by priming (Byrne 2009), this category of social learning does not apply when subjects reproduce a demonstrator's novel action. We observed one anecdote that illustrates cetaceans' natural inclination and ability to copy others' actions. One day, the 2-month-old calf of one of the subjects (Wikie's), who was always by her mother's side, spontaneously produced a half of the untrained behaviour AIR and an accurate match of two behaviours (SO and FW) performed by her. She did so after a delay of 10 and 12 s, respectively (as shown for the latter, FW, in the online resource ESM_4.mpg).

One of the functions that imitation appears to fulfil in some species is primarily social (Bates and Byrne 2010). A strong tendency to imitate the actions of members of your own group may fuel intergroup differentiation and intragroup identity (Byrne 2009; Carpenter 2006; Meltzoff and Decety 2003). Field studies of killer whales have shown that their call structure reflects relatedness and social affiliation (Deecke et al. 2010). Similarly, it has been suggested that killer whales' dietary preferences and foraging behaviours have strong cultural components (Barrett-Lennard and Heise 2007). Certainly, killer whales are remarkably conformists about the type of food they eat (Baird 2000; Barrett-Lennard and Heise 2007). In fact, recently it has been proposed that cultural differences in the form of learned behaviours between ecologically divergent killer whale populations have resulted in sufficient reproductive isolation despite sympatry to lead to incipient speciation (Riesch et al. 2012).

In conclusion, this study adds new data on imitation in a cetacean species, the killer whale, lends further support for action imitation in the delphinids, and raises important questions regarding the evolution of convergent imitation abilities between species as phylogenetically distant as are great apes and cetaceans (Marino 2002). Along with chimpanzees, killer whales and dolphins have occupied a central stage in the animal cultures debate (e.g. Laland and Galef 2009; Laland and Janik 2006, for recent reviews). Field biologists have described several communicative vocal and motor patterns and foraging tactics that display group-specific signatures in cetaceans, mainly in whales and dolphins (Sargeant and Mann 2009; Whitehead 2009;

Yurk 2003). It has been argued that since neither ecological nor genetic factors appear to account for such intergroup differentiation, these apparently fitness-enhancing behaviours are likely to be learned socially, and therefore, they might be interpreted in terms of cultural traditions. This hypothesis has been met with strong opposition (e.g. see commentaries on Rendell and Whitehead's 2001 paper) because the identification of the precise cognitive processes that underpin culture requires experimental approaches (e.g. Galef 2009; Tomasello 2009). The present study shows that killer whales, like bottlenose dolphins, may engage in imitative learning. Additional experiments are needed to further elucidate the nature of killer whales' imitative skills.

Additional details of experimental procedures and five movies are available at Electronic supplementary material.

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