



# Social influence on the expression of robbing and bartering behaviours in Balinese long-tailed macaques

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## Abstract

Animals use social information, available from conspecifics, to learn and express novel and adaptive behaviours. Amongst social learning mechanisms, response facilitation occurs when observing a demonstrator performing a behaviour temporarily increases the probability that the observer will perform the same behaviour shortly after. We studied “robbing and bartering” (RB), two behaviours routinely displayed by free-ranging long-tailed macaques (*Macaca fascicularis*) at Uluwatu Temple, Bali, Indonesia. When *robbing*, a monkey steals an inedible object from a visitor and may use this object as a token by exchanging it for food with the temple staff (*bartering*). We tested whether the expression of RB-related behaviours could be explained by response facilitation and was influenced by model-based biases (i.e. dominance rank, age, experience and success of the demonstrator). We compared video-recorded focal samples of 44 witness individuals (WF) immediately after they observed an RB-related event performed by group members, and matched-control focal samples (MCF) of the same focal subjects, located at similar distance from former demonstrators ( $N = 43$  subjects), but in the absence of any RB-related demonstrations. We found that the synchronized expression of robbing and bartering could be explained by response facilitation. Both behaviours occurred significantly more often during WF than during MCF. Following a contagion-like effect, the rate of robbing behaviour displayed by the witness increased with the cumulative rate of robbing behaviour performed by demonstrators, but this effect was not found for the bartering behaviour. The expression of RB was not influenced by model-based biases. Our results support the cultural nature of the RB practice in the Uluwatu macaques.

**Keywords** Social learning · Response facilitation · Behavioural contagion · Model-based biases · Material culture · Token exchange

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## Introduction

Many animal species use social information, available from conspecifics, to flexibly adjust existing behaviours to particular environmental conditions and learn new behavioural patterns (Duboscq et al. 2016; Hoppitt and Laland 2008). This ability is often locally adaptive, for example when it leads to the acquisition of novel resources (e.g. food, mates), and relies upon phenotypic plasticity (Galef 1995). Unlike individual learning, often stemming from tedious and risky trial-and-error leading to reinforcing rewards or punishments, social learning is defined as the acquisition of novel information or skills that is influenced by the presence, observation of, or interaction with, competent or knowledgeable group members, or their behavioural products (Heyes 1994). Socially mediated information transfer within groups and across generations is at the core of the emergence and

maintenance of behavioural traditions in various animal taxa (Fragaszy and Perry 2003). However, different individual and social learning processes that sustain cultural behaviours are not mutually exclusive and may jointly explain the rise and longevity of animal traditions (Galef 1995).

Cultural transmission is underlain by a number of social learning mechanisms, involving different levels of socio-cognitive complexity (reviewed in Whiten 2000) and associated with multiple psychological biases based on the observer, model and other conspecifics' characteristics (i.e. socially biased learning), or external circumstances (e.g. pay-off bias) (Laland 2004). Among social learning mechanisms, response facilitation is inferred when the observation of a demonstrator performing a behaviour (often resulting in a reward) temporarily increases the probability that the observer will initiate the same behaviour (Hoppitt et al. 2007). The mechanism of response facilitation has, therefore, been proposed to account for matched behaviours and is sometimes approximated to a behavioural contagion (or a "neighbor effect" when the contagion occurs between groups) when two or more animals engage in similar behaviour after being exposed to conspecifics performing that behaviour (Byrne and Russon 1998; Videan et al. 2005). This social influence enhances the expression and the diffusion of specific actions that are either involuntary, reflexive and unlearned (e.g. contagious yawning, self-scratching, predator evasion, contact calls; Amici et al. 2014; Nakayama 2004; Palagi et al. 2014) or voluntary, more elaborate, and learned (e.g. synchronous foraging, grooming, playing, courtship displays; Hoppitt et al. 2007; Nuechterlein and Strorer 1982; Tolman 1964; Zupan et al. 2019). Because the mirror neuron system is likely involved in this social process (Ferrari et al. 2005), response facilitation is characterized by a transient effect (i.e. a response being generally triggered within a few minutes after exposure), even though a more precise timeframe is difficult to establish (Hoppitt et al. 2007). Response facilitation and behavioural contagion are social mechanisms which account for the behavioural synchronization or coordination between the group members, provided that obvious external/internal stimuli causing individuals to perform simultaneously the same act have been ruled out (Hoppitt and Laland 2008). Thus, the social effects of response facilitation and contagion favour the diffusion of novel information and the maintenance of skills/habits at the group level as the product of priming following its display by an initiator (Coussi-Korbel and Frigaszy 1995). In line with the social learning strategies associated with matching behaviours, the identity of the model/demonstrator often matters, with a range of model-based biases (also called "context-biased social learning"), reliant on the model's age (Horner et al. 2010), sex (van de Waal et al. 2010), rank and experience (Kendal et al. 2015), kinship (Wrangham et al. 2016) and social affiliation (Coussi-Korbel

and Frigaszy 1995). Such characteristics of the model may impact response facilitation in various ways (Bono et al. 2018; Botting et al. 2018).

On the one hand, non-human primates, and more specifically macaques, living in highly anthropogenic habitats, such as towns or tourist temple sites, have become generalist, flexible and innovative in their socially learned foraging strategies to compete over and exploit limited access food sources from human-dominated environments (Mangalam and Singh 2013). On the other hand, food provisioning generally relaxes foraging pressure on macaque populations, providing them with free time, conducive to the emergence of various behavioural innovations and traditions; some of them are related to subsistence and can be considered socially transmitted foraging strategy (e.g. bonnet macaques, *Macaca radiata*, engaging in bipedal begging towards tourists; Sinha 2005), whereas others are not immediately beneficial (i.e. adaptive) to their performers, such as playful activities (e.g. Japanese macaques, *Macaca fuscata*, engaging in stone handling behaviour; Leca et al. 2008). In recent years, much attention has been paid to how macaques adjust their behaviour in response to heterogeneous anthropogenic habitats (McLennan et al. 2017), but the origins and the nature of the learning processes involved in the acquisition, expression and diffusion of new behavioural strategies in such environments remain poorly documented.

Food stealing (or scrounging, defined as food transfer occurring between conspecifics despite some resistance from the possessor) is a well-known phenomenon in primates (Brown et al. 2004). Heterospecific kleptoparasitism, including situations where animals steal food and/or objects directly from humans, is increasingly reported in human-modified habitats (Barrett and Henzi 2005). In Asia, for example, urban macaques are frequently seen raiding and snatching food and personal items from people (Radhakrishna et al. 2013). However, it is much rarer to observe a two-step behavioural sequence involving macaques stealing non-edible objects from humans and then exchanging these items for food. In only in a handful of locations, macaques living around temple grounds routinely engage in a group-level foraging strategy called "robbing and bartering" ("RB"; rhesus macaques, *M. mulatta*, at Shimla, India: Chauhan and Pirta 2010; Kaburu et al. 2018; long-tailed macaques, *M. fascicularis*, at Uluwatu, Bali, Indonesia: Brotcorne et al. 2017). During a complete RB sequence, involving a robbing event rapidly followed by a bartering event, a monkey spontaneously steals an inedible object (e.g. eye/sunglasses, hat, sandal) from a temple visitor and uses this object as a token by exchanging it for food with the temple staff. The behavioural sequence may also be incomplete when the robbing event is not followed by any bartering event. The bartering interaction resembles most token exchange tasks experimentally implemented by researchers

in captive settings, in which the symbolic value of a token lies in the quantity and quality of the food reward gained in return (Addessi et al. 2007; Bevacqua et al. 2013; Brosnan and de Waal 2004b; Hopper et al. 2015).

In a recent study, we found that RB in the long-tailed macaques of Uluwatu was a prevalent population-specific behavioural practice characterized by substantial intergroup variation, and persistent over time (i.e. at least 30 years of existence) and across generations of monkeys (Brotcorne et al. 2017). Even though these criteria are often considered a first step in the identification of a behavioural tradition, the second and decisive step towards demonstrating the cultural nature of any behaviour (like RB) is to provide evidence that its expression, transmission, and maintenance are socially mediated (Fragaszy and Perry 2003). In our previous study, we suggested that differences in group demographic structure (e.g. male-biased sex ratio) could partly account for intergroup variation in RB frequency and prevalence (Brotcorne et al. 2017). However, we still do not know whether the expression and maintenance of RB are dependent on social means and, if so, what the underpinning social learning mechanism(s) is/are. Preliminary observations indicated that RB events often occurred in close temporal contiguity within a group, suggesting the existence of a synchrony (or matching) process between individuals in the expression of these behaviours (see video in Online Resource 1). Therefore, could response facilitation and the associated behavioural contagion effect be two social learning mechanisms explaining the synchronized expression of RB? Our study aimed to address this question while discussing the joint role of other learning mechanisms (e.g. stimulus enhancement). Whereas most investigations of response facilitation and behavioural contagion have been conducted on captive subjects engaging in involuntary and simple behaviours (e.g. yawning), our research is one of the first to focus on a learned and relatively complex (i.e. two-stepped) behaviour displayed in a natural setting (see also Fragaszy et al. 2017).

In this study, we aimed to demonstrate that the spontaneous expression of robbing and bartering in the Balinese long-tailed macaques of Uluwatu was socially mediated. Rather than investigating the acquisition or diffusion of these behaviours, we focused on their synchronized expression, (i.e. their behavioural occurrence in response to demonstrators), while controlling for a range of environmental but non-social opportunities to exhibit RB. Although several social learning mechanisms might account for the synchrony in RB behaviours, the protocol used in this study was limited by field constraints and the nature of the data collected did not allow us to empirically discriminate response facilitation and behavioural contagion from other more cognitively complex socially mediated learning mechanisms such as emulation and imitation (Hoppitt and Laland 2008). Conversely, response facilitation is typically tested by comparing the

individual baseline probability to perform a given behaviour with the probability to perform the same behaviour after being exposed to it by a conspecific (Byrne and Russon 1998). In our case, we first tested response facilitation in RB by comparing the rate of these behaviours after witnessing them in at least one demonstrator, with a control condition in which no demonstration occurred. We then tested the contagion-like effect on the RB rates of the witness, as part of an amplification process based on the cumulative effect of observing an increasing rate of RB events performed by demonstrators. Finally, we examined whether model-based biases (i.e. dominance, age, experience and success of the demonstrator) modulated the social learning strategies in robbing behaviour (“who match/copy from whom?”) (Laland 2004). Analysing the role of the demonstrator’s success and its correlated individual characteristics also allowed us to explore the possibility of a socially mediated associative food reinforcement effect, as a complementary explanation for synchronized RB.

We tested six predictions pertaining to the “social influence” hypothesis in the expression of the robbing behaviour and the bartering behaviour. First, a monkey should be more likely to engage in an RB-related behaviour shortly after observing at least one conspecific performing the corresponding behaviour (i.e. a demonstrator) than during a control condition (i.e. without any demonstration; Prediction #1). If supported, this first prediction would be consistent with the response facilitation as an explanatory mechanism of matched RB behaviours. Second, following a contagion-like effect, the rate of RB-related behaviour displayed by a given witness should increase with the cumulative rate of the corresponding behaviour performed by demonstrators (Prediction #2). Third, we explored four types of model-based biases in the expression of RB-related behaviours by witnesses. Given the risky nature of RB, we expected witnesses to “play it safe” by preferentially matching the behaviours of presumably more successful demonstrators. Therefore, a given monkey should be more likely to initiate an RB-related sequence when the demonstrator is a higher-ranking (i.e. dominance-based bias; Prediction #3), older (i.e. age-based bias; Prediction #4), more knowledgeable individual (i.e. experience-based bias; Prediction #5), and when the robbing demonstration was successful (i.e. resulting in the demonstrator acquiring a token and involving a socially mediated reinforcement learning process; Prediction #6).

## Methods

### Study site and population

Uluwatu Temple, located in a dry agricultural landscape of southern Bali, Indonesia (8° 49′ S, 115° 05′ E), is a Hindu

temple complex used by Balinese communities for daily religious ceremonies. It is also one of the most famous touristic spots on the island, visited by 1.5 million tourists in 2015 (W. Wijana, personal communication). A population of long-tailed macaques has lived in this anthropogenic habitat for decades (Fuentes et al. 2005). Based on reliable local sources, the RB practice at this site has been occurring for at least 30 years, though detailed information on its origins is lacking (Brotcorne et al. 2017). In April 2016, the study population comprised 333 long-tailed macaques [55 adult males (> 6 years), 21 subadult males (4–6 years), 79 adult females (> 3.5 years), 20 subadult females (2.5–3.5 years), 94 juveniles (1–4 years for males and 1–2.5 years for females), and 64 infants (< 1 year)] split up into five social groups called Riting, Gading, Celagi, Melum and Tapa. The age categories were based on the reports by Fooden (1995) and Fuentes et al. (2011), and the counting method was described in Brotcorne et al. (2015). The Uluwatu macaques were provisioned daily with a variety of fruits and vegetables by the management team and tourists visiting the temple, allowing for excellent visibility conditions and close-range observation (2–10 m). Overall, this habitat is a human-dominated area characterized by highly frequent interactions with (local and tourist) people, significant human food provisioning, and a very low predation pressure (Brotcorne 2014; McKinney 2015).

## Data collection

Data were collected between September 2015 and August 2016 (over 273 observation days). To test our predictions, two observers (F.B. and A.H.) collected a series of two paired 15-min continuous video-recorded focal animal samples (Altmann 1974), using handheld camcorders (Sony HDR-PJ670), namely a Witness Focal sample (hereafter “WF”, also referred to as “the witness condition”) and a Matched-Control Focal sample (hereafter “MCF”, also referred to as “the control condition”). This WF–MCF paired design was a modified version of the PC–MC method

developed by de Waal and Yoshihara (1983) to study reconciliation in primates.

A WF started immediately after an RB-related event (i.e. either a robbing event, or a complete RB sequence involving a robbing event rapidly followed by a bartering event; see Table 1) displayed by an individual (i.e. the “initial demonstrator”) who was observed by another individual (i.e. the “witness”). The witness became the focal subject. To qualify as a witness, this individual had to be located within 15 meters of the demonstrator and display sustained gaze (i.e.  $\geq 2$  s) towards the demonstrator during the RB-related event. The WFs started opportunistically in conjunction with event sampling sessions (see below) during which the two observers video-recorded RB-related events displayed by potential demonstrators. We stopped event sampling and started a WF when a witness was identified (i.e. when the aforementioned criteria were met). The initial RB-related event performed by a demonstrator was either video- or audio recorded. Once started, the video-recorded WF lasted 15 min or ended earlier if the focal subject was out-of-sight. During WFs, we recorded the identities of the witness and demonstrator, their inter-individual distance at the onset of the WF (i.e. < 1 m, 1 to 5 m, 6 to 10 m, or 11 to 15 m), and all subsequent behaviours performed by the focal subject, including RB-related behaviours. We also recorded any subsequent RB-related behaviours performed by a conspecific (i.e. either the initial or a subsequent demonstrator) that were witnessed by the focal subject within 15 m. The choice of these distance ranges was based on the preliminary data ( $N = 29$  WF) showing that among all the individuals with visual access to a given demonstrator, 93% of these observers had witnessed within 10 m of the demonstrator, 7% within 15 m, and none beyond. When more than one witnesses were present within 15 m of the demonstrator, we selected the closest one. We specified the type (i.e. robbing or bartering) and the outcome (i.e. success or failure) of the RB-related behaviours in both the focal subject and demonstrators (see definitions in Table 1). Moreover, we recorded the type of tokens stolen (e.g. sandal, glasses, hat)

**Table 1** Definitions of RB-related terminology

RB-related term	Operational definition
Robbing	A monkey looks at, rapidly approaches, potentially enters in body contact with a temple visitor and attempts to steal a token from this person before moving away. The robbing outcome may be successful or failed, depending on whether or not the token was taken by the monkey
Bartering	Following a successful robbing event, a monkey attempts to exchange the stolen token for food (reward) with a human barterer (generally a temple staff). The bartering outcome may be successful or failed, depending on whether or not the token was eventually exchanged by the monkey for one or several food items (e.g. fruit, raw egg)
Token	Inedible object without inherent value (e.g. nutritional) for the monkeys, but acts as a secondary reinforcer and acquires a symbolic associative value upon exchange for a food item with a human barterer (Addessi et al. 2007; Brosnan and de Waal 2004a). For the Uluwatu macaques, tokens include sandals, glasses, hats, bag accessories, clothes, and electronics such as phones/cameras



and whether the individual visitor, group of visitors, and tokens targeted by the witness during the WF were the same as the ones previously targeted by the demonstrator.

The paired MCF met a series of conservative criteria to strictly test the influence of the demonstrators in WF on the rate of robbing and bartering behaviours, while controlling for as many other factors as allowed by the field conditions. First, the MCF lasted as long as the paired WF and started on the next possible observation day, when the same focal subject was located within the same distance range of the former initial demonstrator, during the same time block as during the paired WF (i.e. morning or afternoon), and when no RB-related event had occurred at least 5 min before the start of the MCF (i.e. no demonstration in this condition). Second, because the rate of robbing and bartering can be influenced by a range of environmental but non-social opportunities to exhibit RB, we matched, in each WF–MCF pair, the location of occurrence of the events and the density of local visitors who are the primary targets of robbing behaviour (Brotcorne et al. 2017). Using 5-min instantaneous scan sampling (Altmann 1974), we identified the focal subject's location (coded as touristic vs. non-touristic area) and the density of visitors within 15 m (coded as “no visitors”: 0, “low visitor density”:  $\leq 15$  visitors, and “high visitor density”:  $> 15$  visitors). Third, to rule out any response facilitation effect in the control condition, the MCF was discarded if any RB-related behaviour involving a conspecific (i.e. a demonstrator) occurred within 15 m of the focal subject at any time during the MCF. On the basis of these conservative criteria, we collected 117 WF/MCF pairs involving 44 different focal subjects, with 44 witnesses (i.e. three adult females, 26 adult males, 10 subadult males and five juvenile males) from five different groups (i.e. Celagi: 17, Gading: 9, Riting: 9, Tapa: 5, Melum: 4), and 43 demonstrators (one adult female, 28 adult males, 10 subadult males, and four juvenile males) from the same groups (i.e. Celagi: 15, Gading: 9, Riting: 11, Tapa: 5, Melum: 3; Table 2). We collected a mean of  $2.66 (\pm 2.29)$  WF–MCF pairs per focal subject.

## Data analysis

In a previous study, we found intergroup variation in the RB rate in the Uluwatu macaques (Brotcorne et al. 2017). Consequently, we calculated the average frequency of RB-related behaviours for each of the five social groups (i.e. the individual mean number of RB-related events recorded within a group) based on a larger existing dataset ( $N=6283$  RB-related events collected by F.B. and A.H. over 813 h of event sampling; Altmann 1974). We used this value as a cutoff point to assign each focal subject to one of the following three categories of individual baseline frequency of robbing and bartering: “never”: the subject never performed any robbing/bartering behaviour during the study period;

“occasional robber/barterer”: when individual baseline frequency  $\leq$  group average frequency; “frequent robber/barterer”: when individual baseline frequency  $>$  group average frequency. All the focal subjects included in the subsequent analyses were either occasional or frequent robbers (occasional: 40.9%, frequent: 59.1%) and barterers (occasional: 39.0%, frequent: 61.0%). Using dominance matrices generated from 1226.8 h of focal data, we divided the focal subjects into two dominance rank classes (high ranking or low ranking) based on their hourly rates of unidirectional aggressive behaviours performed and received (Table 2). Focal subjects whose observations were insufficient to calculate their rank were excluded from the analysis pertaining to the dominance bias. We defined the population and group-specific robbing prevalence and bartering prevalence as the percentage of individuals (excluding infants) within the Uluwatu population or within each group involved in at least one robbing event and one bartering event (regardless of their outcomes), respectively, recorded during the course of this study. Similarly, we defined the population and group-specific RB rates as the total number of RB events/hour of event sampling time. Finally, the success rate in robbing and bartering was defined as the proportion of events that ended with a successful outcome (see definition of a successful outcome in Table 1).

The inter-observer reliability in data collection between the two observers and video recorders (F.B. and A.H.) was excellent, as measured by the index of concordance ( $O$ ) for categorical variables including monkey identities ( $N=390$  samples,  $O=0.96$ ), age–sex class identification ( $N=350$ ,  $O=0.93$ ), and distances in meters ( $N=200$ ,  $O=0.91$ ). Based on a total of 149 min of video-recorded focal samples, we found a good reliability Cohen's Kappa coefficient ( $k$ ) for the duration and sequence (the overlap in duration and timing of the events was assessed at the nearest second) of all behavioural patterns recorded during focal sampling (average  $k=0.90$ ), including RB-related behaviours ( $k=0.82$ ; Martin and Bateson 1993). All the video-recorded focal samples were scored by F.B. with the data management program The Observer Video-Pro 13© (Noldus Information Technology). The units of analysis were the robbing behaviours and the bartering behaviours displayed by the focal subjects, both grouped under a generic term: “RB-related behaviours”. We tested the social influence on each of these two specific behaviours. Our predictors of interest were the robbing events and the bartering events displayed by demonstrators (i.e. conspecifics watched within 15 m), including the initial RB-related event witnessed by the focal subjects before starting the WF, and possible subsequent RB-related events displayed by demonstrators and witnessed by the focal subjects during the course of the WF which allowed to test for a possible contagion-like effect. We excluded from the data analysis any RB-related behaviours involving edible

**Table 2** List of focal subjects ( $N=44$ ) and demonstrators ( $N=43$ ), with for each of them: identity (ID), sex (F: female, M: male), age class (A: adult, S: subadult, J: juvenile), dominance rank (LR: low-

ranking, HR: high-ranking), individual baseline frequency of robbing and bartering (3 categories: N=never, O: occasional, F: frequent), sampling effort (number of WF–MCF pairs)

Group	Focal subjects (witnesses)							Demonstrators							
	ID	Sex	Age	Rank <sup>b</sup>	Robber cat- egory	Barterer category	WF- MCF pairs	Group	ID	Sex	Age	Rank <sup>b</sup>	Robber cat- egory	Barterer category	WF-MCF pairs
CELAGI	A3	M	A	LR	F	F	2	CELAGI	A3	M	A	LR	F	F	4
RITING	B1	F	A	NA	O	O	1	RITING	B2	F	A	LR	O	N	1
CELAGI	BA	M	A	HR	O	O	1	CELAGI	BA	M	A	HR	O	O	2
RITING	BE	M	S	LR	F	O	2	RITING	BE	M	S	LR	F	O	1
CELAGI	BL	M	J	LR	O	O	1	CELAGI	BL	M	J	LR	O	O	1
GADING	BT	M	A	HR	O	O	1	RITING	CT	M	A	HR	F	F	2
RITING	C1 <sup>a</sup>	F	A	NA	O	N	2	RITING	CC	M	A	LR	F	F	12
MELUM	C2	M	A	NA	O	O	1	RITING	DA	M	A	HR	O	O	1
RITING	CC	M	A	LR	F	F	7	TAPA	DB	M	A	LR	F	F	6
RITING	CT	M	A	HR	F	F	1	MELUM	FE	M	A	NA	F	F	1
TAPA	DB	M	A	LR	F	F	2	CELAGI	JK	M	J	LR	O	O	2
TAPA	JB	M	A	LR	F	F	1	CELAGI	M1	M	S	LR	F	F	2
CELAGI	JK	M	J	LR	O	O	1	CELAGI	M2	M	S	LR	F	F	4
GADING	KD	M	S	LR	O	O	1	MELUM	MR	M	A	NA	F	F	2
CELAGI	M1	M	S	LR	F	F	4	CELAGI	MA	M	A	HR	O	O	1
CELAGI	MA	M	A	HR	O	O	1	MELUM	MM	M	A	NA	F	F	1
GADING	MD	M	J	LR	F	F	1	TAPA	MP	M	S	LR	O	O	1
TAPA	MP	M	S	LR	O	O	4	CELAGI	MT	M	A	LR	F	F	5
MELUM	MR	M	A	NA	F	F	1	CELAGI	N3	M	A	HR	F	F	4
CELAGI	MT	M	A	LR	F	F	2	CELAGI	NS	M	A	HR	F	F	9
CELAGI	N3	M	A	HR	F	F	3	TAPA	NY	M	A	LR	F	F	4
CELAGI	NJ	M	S	HR	O	O	2	GADING	PA	M	A	HR	O	O	1
CELAGI	NS	M	A	HR	F	F	6	CELAGI	PE	M	J	LR	O	O	1
CELAGI	NT <sup>a</sup>	F	A	NA	O	N	1	RITING	PP	M	S	LR	F	O	3
TAPA	NY	M	A	LR	F	F	5	GADING	PS	M	A	HR	F	F	5
CELAGI	PE	M	J	LR	O	O	1	RITING	RB	M	S	HR	F	F	2
MELUM	PN	M	A	NA	O	O	1	RITING	RW	M	S	HR	F	F	8
RITING	PP	M	S	LR	F	O	5	TAPA	RM	M	A	HR	F	F	2
GADING	PS	M	A	HR	F	F	4	TAPA	RC	M	A	LR	F	F	1
CELAGI	RF <sup>a</sup>	M	A	LR	O	N	1	GADING	RG	M	A	LR	O	F	1
GADING	RG	M	A	LR	O	F	1	GADING	S	M	A	LR	F	F	1
TAPA	RM	M	A	HR	F	F	2	CELAGI	SM	M	A	HR	F	F	2
RITING	RW	M	S	HR	F	F	11	GADING	SG	M	A	HR	F	F	3
GADING	S	M	A	LR	F	F	1	RITING	SR	M	J	LR	O	O	2
GADING	SG	M	A	HR	F	F	2	CELAGI	ST	M	S	LR	F	F	5
CELAGI	SM	M	A	HR	F	F	2	RITING	SJ	M	A	LR	O	O	1
RITING	SR	M	J	LR	O	O	2	RITING	SB	M	A	LR	F	F	2
CELAGI	ST	M	S	LR	F	F	4	CELAGI	TW	M	A	HR	F	F	1
MELUM	TT	M	A	NA	F	F	1	RITING	VI	M	S	LR	F	F	4
UPTAIL	UT	M	J	LR	O	O	4	GADING	WY	M	S	HR	F	F	3
RITING	VI	M	S	LR	F	F	7	GADING	WH	M	A	LR	F	F	1
GADING	WL	M	A	HR	F	F	2	GADING	WL	M	A	HR	F	F	1
CELAGI	WS	M	A	LR	F	F	8	CELAGI	WS	M	A	LR	F	F	1
GADING	WY	M	S	HR	F	F	4								

<sup>a</sup>Focal individuals not identified as barterers (“Level 0”) during the course of the study ( $N=3$ ). <sup>b</sup>NA: individuals for which the rank could not be measured

items (e.g. food, drinks in plastic bottles), because we were interested in testing the social influence on a phenomenon involving a secondary reinforcement process, rather than a primary one.

Stealing an object from a human and possibly exchanging it for food is a complex sequence involving several behavioural patterns that are likely underpinned by distinct mechanisms. To investigate the social influence on the expression of robbing and bartering behaviours separately, we ran two different models, one for each behavioural component. To test Prediction #1 and Prediction #2, we ran generalized linear mixed models (GLMM) and set the frequency of robbing or the frequency of bartering performed by the witness as response variables. We included the observation time (i.e. the duration in minutes of WF and MCF samples) as an offset term to adjust for differential exposure time. Therefore, the frequencies of robbing or bartering were converted into rates per minute. We included in the GLMMs two fixed predictors of interest corresponding to each of the first two predictions related to social influence: the condition (WF: with at least one demonstrator vs. MCF: without any demonstration), and the cumulative rate of robbing vs. bartering behaviours performed by demonstrators (computed as the total frequency of robbing demonstration vs. bartering demonstration occurring during a WF or MCF and converted into rate per minute of observation time). Besides the two predictors of interest, we wanted to control for the potential influence of external and internal variables not related to social influence. Therefore, we included several fixed control predictors: (1) the density of visitors (“low” vs. “high”), (2) the interaction between the density of visitors and the condition (WF vs. MCF), and (3) the individual baseline frequency of RB-related behaviours of the focal subject (“occasional” vs. “frequent”). Finally, we accounted for the paired structure of the study design and within-focal subject repeated observations by including as random effect factors the identity of demonstrator/witness pairs and the identity of witnesses, respectively. To select the best GLMM family, we first tested for the best fitted distribution (i.e. Poisson vs. negative binomial vs. zero-inflated Poisson) to model robbing and bartering count data using the R-package “fitdistrplus” (Delignette-Muller and Dutang 2015) and the analysis of the Pearson residuals distribution. Then, we chose the negative binomial family (with the log link function) for the robbing and the bartering models that we fitted with the “glmer.nb” function in the R-package “lme4” (Bates et al. 2015). We checked for the collinearity of predictors with the VIF function and the overdispersion assumptions of the models (Bates et al. 2015). We excluded from the analyses individuals that were not identified as robbers or barterers (cf. category “never” of the individual baseline frequency of RB-related behaviours). A total of 234 observations involving 44 focal subjects in 117 WF–MCF pairs contributed to

the robbing model, and 226 observations involving 41 focal subjects in 113 WF–MCF pairs contributed to the bartering model. For goodness-of-fit, we used the likelihood-ratio chi-squared test (LRT) to compare the full model against the null model that included the intercept and random effects to assess the significance of the full model (Forstmeier and Scheelzeth 2011). Moreover, we similarly used LRTs comparing the full model against reduced models excluding the fixed predictors of interest to assess their contribution and specific influence on the response, with the control predictors and random effects held constant (Bolker et al. 2009). The statistics presented include the estimates  $\pm$  standard error and  $p$  values associated with the Wald Z tests of the full model table, and the  $\chi^2$  and  $p$  values from the LRTs comparing the full with null/reduced models. We also reported mean values and standard deviations when necessary.

To determine the timing of any possible social influence, we descriptively analysed how fast focal subjects initiated an RB-related sequence after watching a demonstrator. To do so, we fit a cumulative incidence plot of robbing behaviour (i.e. the first part of any RB-related sequence) in relation to the time elapsed from the onset of the WF, using the “cuminc” function of the R-package “cmprsk” (Gray 2015). WF samples in which no robbing behaviour was performed by focal subjects by the end of the observation period were right-censored (i.e. 29.9% of WF samples). In other words, these observations were not ignored but handled as “failures” (cf. Jahn-Eimermacher et al. 2011) because the robbing latency outcome (time-to-event) was incompletely determined (i.e. considered to be at least as long as the duration of the observation time) (Fox 1993).

To investigate a possible stimulus enhancement process in the expression of robbing behaviour, we tested whether, after witnessing an RB-related event, a focal subject targeted, at least more than expected than chance (expected probabilities: 0.5), the same/different (groups of) visitors and tokens as/from the ones previously targeted by the demonstrators. We used exact binomial tests on the frequencies of different types of (groups of) visitors (same vs. different) targeted in WF samples, and the McNemar–Bowker test to analyse the association between the type of tokens stolen by demonstrators and then by witnesses (Agresti 2007).

To test the model-based biases, we fitted a GLMM (mixed logistic regression model, with “glmer” of the R-package “lme4”; Bates et al. 2015) with the probability for a given witness to rob (i.e. initiate an RB-related sequence) during the WF condition. This probability was treated as the response variable. The dominance rank (“low-ranking” vs. “high-ranking”; Prediction #3), age (“immature” vs. “adult”; Prediction #4), prior experience (i.e. individual baseline frequency of robbing behaviour: “occasional” vs. “frequent”; Prediction #5) of the demonstrator were added as fixed effects. To test whether the dominance-based bias and the

age-based bias vary with the rank and age of the witness, we added the interactions of these variables across demonstrators and witnesses. Moreover, we included the outcome of the robbing demonstration (“success” vs. “failure”; see Table 1) as another fixed predictor in the model-based biases to test whether a given witness was more likely to initiate an RB-related sequence when the demonstrator was successful in acquiring a token at the end of the robbing phase (Prediction #6). The identities of the witnesses and demonstrators were added as random factors to account for within-subject repeated events. Here, we only used observations from the WF condition, i.e. when a demonstrator was present. Moreover, we selected observations in which the social influence on the witness was unequivocally attributed to a single demonstrator engaged in robbing. Therefore, we analysed the relationships between the witness and the initial demonstrator by removing from the dataset a proportion (23.1%) of the WF samples in which several subsequent demonstrators might have influenced the witness before the witness engaged in a first robbing event.

Finally, to better understand potential model-based biases in the expression of RB-related behaviours, we also analysed to what extent the aforementioned individual characteristics could account for the demonstrator’s RB-related success. Therefore, we assessed the variance in the proportion of success in robbing demonstrations and bartering demonstrations (i.e. the number of success outcome relative to the number of attempt as response variable) as a function of the demonstrator’s dominance rank, age, and prior experience (i.e. three categorical predictors), using a logistic regression model (GLM binomial with “glm” function of the R-package “car”). We performed all (two-tailed) statistical analyses using R 3.4.3 (R Core Team 2013), with a confidence interval set at 95%.

## Results

The RB-related behavioural practice in the Uluwatu population of long-tailed macaques occurred frequently (population-specific rate: 7.78 robbing events/hour and 3.26 bartering events/hour) and was prevalent (49.3% of population members performed robbing behaviour and 35.6% performed both robbing and bartering behaviours). We found some intergroup variation in the rate of robbing (Celagi: 8.78, Riting: 8.10, Gading: 6.46, Melum: 6.85, Tapa: 6.67 events/h), the rate of bartering (Celagi: 3.62, Riting: 3.26, Gading: 2.80, Melum: 3.43, Tapa: 2.84 events/h), the robbing prevalence (Celagi: 62.1%, Riting: 68.3%, Gading: 64.3%, Melum: 27.1%, Tapa: 31.1%), and the bartering prevalence (Celagi: 44.8%, Riting: 39.0%, Gading: 53.6%, Melum: 22.9%, Tapa: 17.8%).

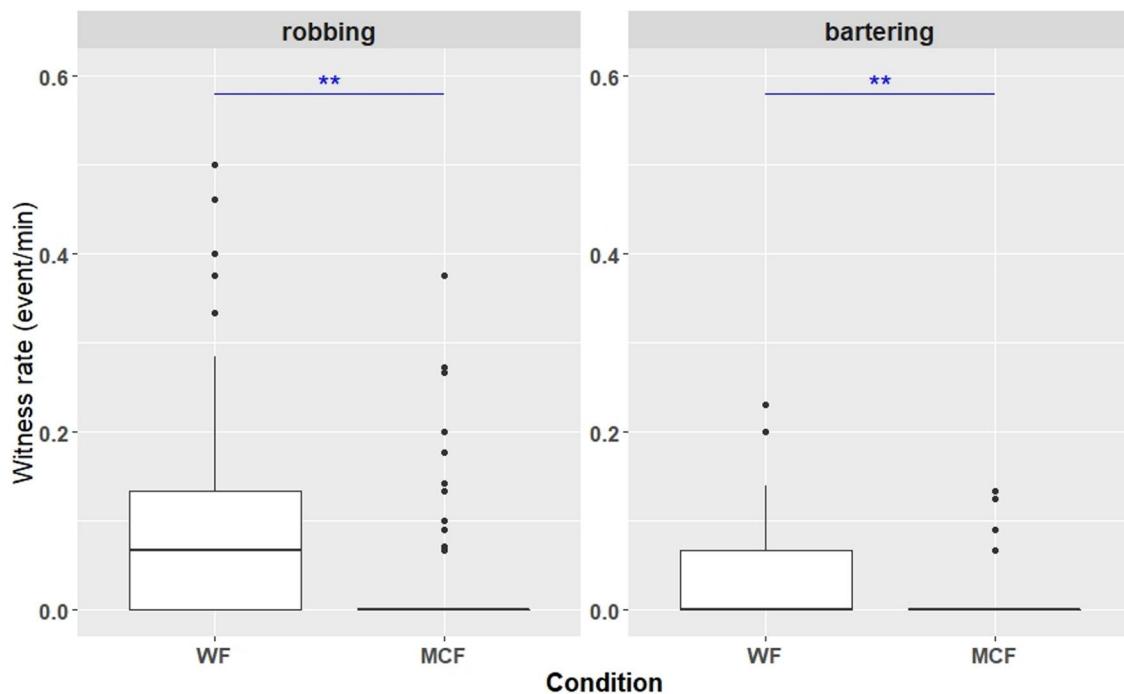
Robbing behaviour performed by the witnesses during WF samples was consistently more frequent (70.1% of WF vs. 20.5% of MCF) than bartering behaviour (32.5% of WF vs. 5.1% of MCF). Regarding the outcome of these behaviours displayed by the demonstrators and the focal subjects during WF and MCF, 47.1% of the 376 robbing events ended with a successful outcome, and 77.2% of the 127 bartering events ended with a successful outcome.

## Social influence on the expression of robbing behaviour

The full GLMM model testing the effect of predictors accounting for social influence (i.e. the condition and the cumulative rate of robbing events performed by demonstrators), and the effect of control predictors, on the focal subject’s robbing rate was statistically significant (LRT:  $\chi^2_5 = 68.08$ ,  $p < 0.001$ ). More specifically, robbing behaviour was more frequently performed by the focal subject in WF than in MCF (mean robbing rate/min  $\pm$  SD =  $0.11 \pm 0.15$  and  $0.03 \pm 0.07$ , respectively; Fig. 1, Table 3a). The condition had a significant effect on the robbing rate of focal, with other predictors held constant (LRT full-reduced model:  $\chi^2_2 = 14.68$ ,  $p < 0.001$ ). Therefore, the part of Prediction #1 (i.e. response facilitation) pertaining to the robbing behaviour was supported (see Online Resource 2 for an example of response facilitation in the witness condition). Regarding the control predictors, the rate of robbing behaviour performed by the focal subject significantly increased with the density of visitors ( $p < 0.05$ ), and with its individual baseline frequency of robbing behaviour (i.e. robbing rates were higher in frequent robbers than in occasional robbers,  $p < 0.01$ , Table 3a). However, the interaction between the condition and the visitor density was not statistically significant ( $p = 0.69$ ), which means that the effect of response facilitation on the expression of robbing behaviour by witnesses was constant regardless of the visitor density (Table 3a). Moreover, the rate of robbing behaviour performed by the witness significantly increased with the cumulative rate of robbing behaviours exhibited by demonstrators (Fig. 2a, Table 3a); this effect was significant with other predictors held constant (LRT full-reduced model:  $\chi^2_1 = 6.72$ ,  $p < 0.01$ ). Compared to a condition where there was no demonstration, the rate of robbing behaviour performed by witnesses increased by three and by five when, respectively, one and five robbing events occurred nearby. This result was consistent with a contagion-like effect on the expression of robbing behaviour. Therefore, the part of Prediction #2 pertaining to the robbing behaviour was supported.

The response facilitation following the witnessing of a robbing behaviour was fast. Indeed, within the first minute of the WF, 39.3% of the focal subjects already engaged in robbing behaviour after watching a demonstrator (Fig. 3).





**Fig. 1** Boxplot (with median) comparing the rate of robbing (left graph) and bartering (right graph) (number of behaviour per minute) performed by the focal subjects in the witness condition (WF) vs. matched-control condition (MCF) (\*\* $p < 0.01$ )

**Table 3** Generalized linear mixed models (mixed negative binomial regression) on (a) robbing and (b) bartering rates testing the fixed effect of social influence (i.e. condition: witness focal or WF vs. matched-control focal or MCF, and cumulative rate of robbing and bartering events performed by demonstrators) and control predictors (i.e. visitor density: “weak” vs. “high”, and robber/barterer baseline category: “occasional” vs. “frequent”)

Response variable	Fixed effects	Estimate ( $\beta$ ) $\pm$ SE	Z value	p value
(a) Robbing	Intercept	$-4.56 \pm 0.31$	$-14.54$	$< 0.001$
	Condition <sup>a</sup>	$0.83 \pm 0.26$	$3.18$	$< 0.01$
	Cumulative rate of robbing by demonstrators	$2.13 \pm 0.79$	$2.70$	$< 0.01$
	Robber category <sup>b</sup>	$0.86 \pm 0.28$	$3.10$	$< 0.01$
	Visitor density <sup>c</sup>	$0.68 \pm 0.32$	$2.15$	$< 0.05$
	Condition:visitor density	$-0.15 \pm 0.36$	$-0.40$	$0.69$
(b) Bartering	Intercept	$-6.79 \pm 0.67$	$-10.06$	$< 0.001$
	Condition <sup>a</sup>	$1.59 \pm 0.56$	$2.83$	$< 0.01$
	Cumulative rate of bartering by demonstrators	$0.84 \pm 1.86$	$0.45$	$0.65$
	Barterer category <sup>b</sup>	$1.48 \pm 0.51$	$2.88$	$< 0.01$
	Visitor density <sup>c</sup>	$0.70 \pm 0.76$	$0.92$	$0.36$
	Condition:visitor density	$0.01 \pm 0.82$	$0.02$	$0.99$

The observation time was included as an offset term (correcting frequencies into rates per minute). The table shows parameter estimates, standard errors, Z test values and  $p$  values for the full model components

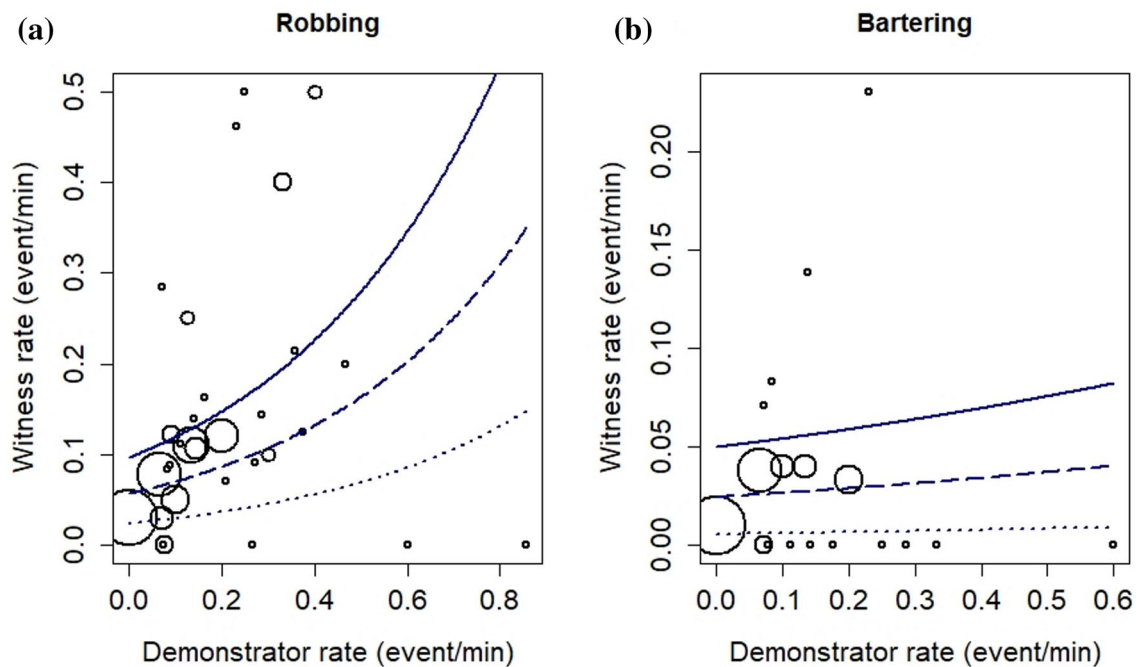
<sup>a</sup>“MCF” as reference category

<sup>b</sup>“Occasional” as reference category

<sup>c</sup>“Weak” as reference category

Within the first three minutes, more than half of the focal subjects (52.1%) engaged in robbing behaviour. Finally, 70.1% of the focal subjects engaged in robbing behaviour by the end of the observation time. Therefore, amongst the 82 cases (out of 117) in which the robbing response has been facilitated, 56.1% was triggered within a minute,

68.3% within two minutes, and three-fourths (74.4%) by three minutes. Therefore, the response facilitation was mainly effective during the first three minutes following the witnessing of a robbing behaviour, with a sharp peak during the first minute.



**Fig. 2** Mean rate of **a** robbing or **b** bartering behaviour performed by witnesses as a function of the cumulative rate of the corresponding behaviour performed by demonstrators, and prediction lines of the negative binomial GLMMs (solid line: condition = “WF”, visitor density = “high”, baseline RB frequency = “frequent”; dashed line: condition = “WF”, visitor density = “weak”, baseline RB frequency = “frequent”; dotted line: condition = “WF”, visitor density = “weak”,

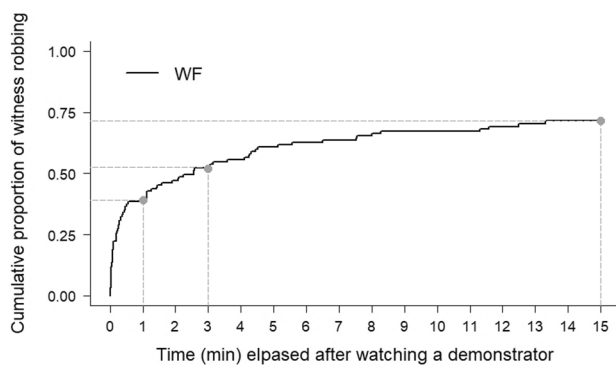
baseline RB frequency = “occasional”). Because many individual data points were overlapping, we drew the bubble points from the mean rates of robbing and bartering behaviours performed by witnesses for every demonstrator rate, and the bubble size corresponds to a log-transformation of the number of witness observations (the largest one corresponds to 119, the smallest ones to 1)

In the WF condition, the focal subjects were significantly more likely to target visitors and groups of visitors that were different from the ones previously targeted by the demonstrators (Binomial tests, expected probabilities: 0.5:  $N_{\text{different visitor}} = 95$ ,  $N_{\text{same visitor}} = 25$ ,  $p < 0.001$ ;  $N_{\text{different group}}$

$= 77$ ,  $N_{\text{same group of visitor}} = 43$ ,  $p < 0.01$ , respectively). Because a variety of tokens were involved in RB-related events, we also assessed whether the witnesses preferentially targeted the same category of tokens as the ones previously targeted by demonstrators, at least more than dictated by chance. We did not find any statistically significant results: the focal subjects did not target tokens (sandals: 39.0%, glasses: 30.5%, hats: 13.6%, electronics, such as phones/cameras: 11.9%, and bag accessories: 5.1%) that were similar to the ones previously targeted by demonstrators (McNemar–Bowker test:  $\chi^2_{10} = 9.11$ ,  $p = 0.52$ ). Both results were not consistent with the hypothesis whereby the matched expression of robbing behaviours would be stimulus-specific.

### Social influence on the expression of bartering behaviour

The full GLMM testing the effect of predictors accounting for social influence (i.e. the condition and the cumulative rate of bartering events performed by demonstrators), and the effect of control predictors, on the focal subject’s bartering rate was statistically significant (LRT:  $\chi^2_5 = 46.33$ ,  $p < 0.001$ ). More specifically, bartering behaviour was significantly more frequently performed by



**Fig. 3** Cumulative incidence plot of first robbing behaviour performed by the focal subjects after watching a demonstrator (i.e. in the witness condition—WF). The curve represents the observed latency and dashed grey lines represent the proportion of robbing after 1, 3 and 15 min elapsed from the time the witness watched the demonstrator

the focal subject in WF than in MCF (mean bartering rate/min =  $0.03 \pm 0.05$  and  $0.01 \pm 0.02$ , respectively; Fig. 1, Table 3b), with other predictors held constant (LRT full-reduced model:  $\chi^2_2 = 17.89$ ,  $p < 0.001$ ). Regarding the control predictors, the rate of bartering behaviour performed by the focal subject significantly increased with its individual baseline frequency of bartering behaviour (i.e. bartering rates were higher in frequent barterers than in occasional barterers,  $p < 0.01$ ), but not with the density of visitors ( $p = 0.36$ ; Table 3b). Consistently, and in line with what we found for the robbing behaviour, the interaction between the condition and the visitor density was not statistically significant ( $p = 0.99$ ). Therefore, the part of Prediction #1 (i.e. response facilitation) pertaining to the bartering behaviour was supported. Contrary to what we found for the robbing behaviour, the rate of bartering behaviour performed by the focal subject did not significantly increase with the cumulative rate of bartering behaviours exhibited by demonstrators (Fig. 2b, Table 3b), with other predictors held constant (LRT full-reduced model:  $\chi^2_2 = 0.18$ ,  $p = 0.91$ ). Therefore, the part of Prediction #2 pertaining to the bartering behaviour was not supported.

### Model-based biases

To test model-based biases, we analysed whether the demonstrator's characteristics influenced the matched response of the witness. We found that dominance rank, age, prior experience and robbing success of the demonstrator had no significant effect on the probability of the witness initiating an RB-related sequence (LRT full-null model:  $\chi^2_8 = 10.39$ ,  $p = 0.24$ , Table 4). Therefore, Predictions #3, 4, 5, and 6 were not supported. Moreover, the interactions between the dominance rank and age of the witness and that of the demonstrator on the expression of an RB-related sequence by witnesses were not statistically significant (Table 4).

Finally, we tested whether the individual characteristics of the demonstrators (i.e. dominance rank, age, and prior experience) were related to their own proportion of success in performing RB-related behaviours. With regard to robbing behaviour, the full GLM model was statistically significant (LRT full-null model:  $\chi^2_3 = 13.55$ ,  $p < 0.01$ ). More specifically, frequent robbers showed higher proportions of robbing success than occasional robbers (estimate  $\pm$  SE =  $1.38 \pm 0.45$ ,  $p < 0.01$ ), whereas dominance rank (estimate  $\pm$  SE =  $0.17 \pm 0.35$ ,  $p = 0.62$ ) and age (estimate  $\pm$  SE =  $0.24 \pm 0.35$ ,  $p = 0.49$ ) had no significant influence. As for bartering behaviour, the demonstrator's characteristics did not significantly influence its proportion of success (LRT full-null model:  $\chi^2_3 = 0.64$ ,  $p = 0.88$ ).

**Table 4** Generalized linear mixed model (mixed logistic regression) of the model-based biases: effects of the demonstrator characteristics (i.e. dominance rank, age, prior experience and robbing success during demonstration), their interactions with the witness characteristics, on the probability for the witness to initiate an RB-related sequence

Fixed effects	Estimate ( $\beta$ ) $\pm$ SE	Z value	p value
Intercept	$0.01 \pm 1.07$	0.01	0.99
Demonstrator's age <sup>a</sup>	$1.26 \pm 0.70$	1.70	0.09
Demonstrator's dominance rank <sup>b</sup>	$0.09 \pm 0.63$	0.14	0.89
Demonstrator's robbing frequency <sup>c</sup>	$-0.62 \pm 0.88$	-0.66	0.51
Witness' age <sup>a</sup>	$1.84 \pm 0.89$	1.96	0.05
Witness' dominance rank <sup>b</sup>	$0.22 \pm 0.67$	0.30	0.76
Demonstrator's age $\times$ witness' age <sup>a</sup>	$-1.96 \pm 1.06$	-1.74	0.08
Demonstrator's rank $\times$ witness' rank <sup>b</sup>	$0.87 \pm 1.11$	0.74	0.46
Demonstrator's success	$0.02 \pm 0.60$	0.04	0.97

Reference categories: <sup>a</sup>“Immature”; <sup>b</sup>“Low-ranking”; <sup>c</sup>“Occasional”

### Discussion

We tested a series of predictions pertaining to several forms of social influence on the expression of robbing and bartering behaviours in the free-ranging Balinese long-tailed macaques at Uluwatu Temple. More specifically, the main goal was to examine whether the synchronized expression of these behaviours could be explained by response facilitation and behavioural contagion, and whether these social processes were influenced by model-based biases. First, we found that an individual was significantly more likely to engage in either robbing or bartering behaviours shortly after observing at least one conspecific performing the same behaviour than during a control condition (i.e. without any demonstration). The witnesses were clearly facilitated in their responses, as they started exhibiting RB-related behaviours almost four times more frequently in the vicinity of a demonstrator already engaged in this activity than in the absence of any demonstration. This result supports the hypothesis that response facilitation is one of the processes of social influence accounting for the matched expression of robbing and bartering behaviours. Second, response facilitation had a rapid effect, with more than half of the focal subjects engaging in robbing behaviour within 3 min after watching a demonstrator performing this behaviour. Third, we found that the rate of robbing behaviour performed by the witness significantly increased with the cumulative rate of robbing behaviours exhibited by demonstrators. These social effects were not found for the bartering behaviour. These results were indicative of a behavioural contagion-like effect in the expression of robbing (but not bartering) behaviours. Fourth, these social effects were sustained even

after controlling for external variables related to environmental opportunity (i.e. the density of temple visitors, who are the primary targets of robbing behaviour). Fifth, even though the expression of RB-related behaviours was consistent with response facilitation, we did not find any evidence that this effect was dependent on the dominance status, age, prior experience and success of the demonstrators, as well as on any interactions between the social rank and age of the witnesses and that of the demonstrators. Overall, we provided the first solid and converging pieces of evidence that the spontaneous expression of robbing and bartering in wild macaques was socially mediated and parsimoniously explained by response facilitation, even though this social effect was not markedly biased by the demonstrator's individual characteristics and success. However, our findings do not rule out several other social learning mechanisms that might play a complementary role in the synchronous display of RB-related behaviours.

We showed that the rates of expression of robbing and bartering behaviours consistently increased after exposure to at least one demonstrator displaying similar behaviours. This result is the first step in demonstrating the explanatory role of response facilitation in the synchronized expression of robbing and bartering within a group (cf. Hoppitt and Laland 2008). Response facilitation also accounts for the synchronization process underpinning the collective performance of fur rubbing behaviour in white-faced capuchins (*Cebus capucinus*; Meunier et al. 2008) and object play in pigs (*Sus scrofa domesticus*; Zupan et al. 2019), after these behaviours have been initiated by conspecific demonstrators. A second piece of evidence supporting the effect of response facilitation in our study lies in the timeline of the social influence on the expression of robbing behaviour. This effect peaked during the first minute following exposure and was still significant for two additional minutes. It persisted even longer, albeit with a lower intensity. A similarly rapid response facilitation was found in the synchronized expression of other types of behaviour in various animal taxa, including preening in domestic fowls (*Gallus gallus domesticus*; Hoppitt et al. 2007), feeding in pig-tailed macaques (*M. nemestrina*; Ferrari et al. 2005), and yawning in bonobos (*Pan paniscus*) and humans (*Homo sapiens*) (Palagi et al. 2014). From a neurophysiological perspective, the short-lived quality of response facilitation could be underlain by the molecular functioning of mirror neurons, whose activity is immediately turned on when an individual is performing an action, and when this individual is observing the same action being performed by another individual (Ferrari and Cribari-Neto 2004; Hoppitt and Laland 2008).

We found evidence for an amplification process in this social influence. Indeed, the probability for a given witness to engage in robbing (but not bartering) behaviour significantly increased with the cumulative rate of robbing

behaviours performed by local demonstrators. Thus, a contagion-like process is likely to account for the quasi-simultaneous expression of robbing behaviour among several group members, and the occurrence of bartering behaviour might simply *appear* to be synchronized, as it was generally a second step following the facilitated robbing response (cf. Coussi-Korbel and Frigaszy 1995; see Online Resource 2).

In our attempt to test whether the synchronized performance of robbing behaviours could be partly explained by obvious non-social stimuli, we found that the social influence on the expression of this collective phenomenon was not significantly affected by the local density of visitors. Just as dawn song in birds can be triggered by specific environmental stimuli (e.g. variation in light intensity) independently of conspecifics' behaviour (Hoppitt and Laland 2008), the variation over time in the density of visitors could be viewed as a key environmental factor influencing RB opportunities at the individual and group levels, independently of any social context. However, our results indicate that the presence of demonstrators was sufficient to explain the synchronization in the performance of robbing behaviours among group members, regardless of the availability in tokens (proxied by the visitor density). Finally, considering the large amount of frequently and widely distributed food at this study site (Brotcorne et al. 2017), the bursts of synchronized RB behaviours in the witness condition are not likely to be explained by sudden and independent changes in the hunger-related motivation of these macaques. However, only a thorough analysis of specific physiological or behavioural correlates of hunger would allow us to be more conclusive.

Given the presumably adaptive nature of RB behaviour, we argue that behavioural synchrony in robbing could be beneficial for these macaques. First, the socially aided maintenance (and possibly learning) of this unique two-stepped foraging strategy may play a vital role in the acquisition of energy-rich food (typically obtained by the monkeys after successful bartering events) in this anthropogenic environment where natural food is sparse (Brotcorne et al. 2017). Second, the Uluwatu macaques may take advantage of the local and temporary context of human confusion and emotional disturbance typically associated with an ongoing RB event to target distracted and thus less vigilant visitors. Third, such a temporal and spatial behavioural coordination among conspecifics may promote social cohesion at the group level (Coussi-Korbel and Frigaszy 1995; Duranton and Gaunet 2016). All these hypotheses deserve further investigation to assess the RB-related nutritional gains (e.g. by comparing food intakes across individuals performing RB at different rates) and social benefits (e.g. by testing the correlation between individual centrality within the social network and individual RB performance).

Even though we found a response facilitation of the expression of RB-related behaviours in the Uluwatu

macaques, and a contagion-like effect on the performance of robbing behaviour, these processes of social influence were not significantly modulated by the demonstrator's dominance rank, age, experience, and success. This result is not consistent with the growing body of evidence that the matching expression of behaviours in primates and other social animal taxa is often not random but socially dependent on the identity of the models (Fragaszy and Visalberghi 2004). Nevertheless, model-biased learning has been mainly tested and demonstrated as a mechanism underlying the emergence and early diffusion of innovative behaviours, such as novel food-processing techniques or the adoption of new food items into the diet (Laland 2004). Our study did not meet these conditions because the RB-related behavioural practice has been established in this monkey population for at least three decades (Brotcorne et al. 2017). This may partly explain why we did not find a significant model-based bias in the daily expression of RB. In accordance with the “social conformity” hypothesis (Laland 2004), the “follow-the-majority” behavioural strategy could be more effective, or cognitively easier to implement, in the synchronized expression of the RB practice than dominance- or age-based biases. Our results showed a contagious expression of robbing behaviour which was consistent with a positive frequency-dependent social learning, whereby the rate of occurrence of a given behaviour within a group had a cumulative facilitating effect on the response among witnesses. Conformity-biased learning has also been shown to maintain population-level food preference in chimpanzees (Hopper et al. 2011). In the context of the socially maintained RB practice, the Uluwatu macaques might have developed such frequency-dependent biases rather than model-based ones because higher-ranking or older individuals were not necessarily more skilled RB models. Indeed, we found that prior experience of the demonstrators was a good predictor of their robbing success, but not dominance rank and age, and none of these factors had a significant influence on their bartering success. However, much care is required when discussing these results, due to our relatively limited sample (i.e. 234 robbing events and 226 bartering events). The question of the individual variation in robbing and bartering performance should be further investigated with a larger data set.

Because tokens (e.g. sandals, glasses, hats) are first stolen by the monkeys and then exchanged for food rewards, the acquisition and maintenance of RB-related behaviours could also partly rely on cognitively simple conditioning mechanisms based on a secondary reinforcement process (cf. Galef 1995). Reinforcement learning can occur through individual experience, or by observing the outcome of conspecifics' behaviours (Galef 2013). The latter scenario is referred to as “observational conditioning”, whereby the observation of a demonstrator's behaviour draws the witness's attention to the food reinforcer

received by the demonstrator (rather than to the behaviour itself), leading to associative learning which may elicit a similar response by the witness (Zentall 1996). Nevertheless, we found that the demonstrator's relative success in robbing behaviours—which could inform the witness on the likelihood of obtaining a secondary reinforcer (i.e. a token) and then a primary reinforcer (i.e. food reward) when performing RB-related sequences—had no significant effect on the witness' probability to initiate an RB-related sequence. We acknowledge that this result alone is not sufficient to claim that the expression of RB is not underlain by any reinforcement learning. Further analysis focusing on the type and effects of reinforcers associated with RB is necessary to address this question.

Finding evidence for response facilitation as an explanatory process in the synchronous expression of RB-related behaviours does not rule out the possible joint role of other (more or less complex) learning processes in their acquisition and maintenance. Compared to other social learning mechanisms, like imitation and emulation, response facilitation has received little attention in the literature, especially in free-ranging animals. This is probably because testing and discriminating the effect of alternative social learning mechanisms are challenging, as it requires controlling for the simultaneous influence of several external stimuli on the expression of a given behaviour across multiple group members (Hoppitt et al. 2007). For example, the expression of a learned behaviour may be stimulus-specific, that is underlain by stimulus/local enhancement, whereby the activity (e.g. foraging) of a conspecific attracts the observer's attention toward a particular object/area (e.g. food item/patch) about/in which the subject will learn by itself (Whiten 2000). Our results showed that the social stimulation effect on the expression of RB-related behaviours was action-specific (i.e. partly explained by response facilitation). Moreover, we found that witnesses did not tend to target the same (group of) visitors and type of tokens as those previously targeted by the demonstrators. This result suggests that stimulus enhancement is not a primary social learning mechanism underpinning the expression of RB. This is consistent with reports on diet acquisition in tufted capuchins: not only naïve subjects did not preferentially target the type of novel food eaten by conspecifics (Visalberghi and Addessi 2001), but they actually increased their feeding activities on unfamiliar food items after witnessing conspecifics feeding on familiar food items (Visalberghi and Addessi 2000). However, the exact role of stimulus enhancement in the synchronous expression of RB-related behaviours deserves further investigation to systematically compare the effect of a socially influenced attraction towards specific stimuli pertaining to different RB situations, such as silent versus loud temple visitors, or half-hidden versus visually conspicuous tokens targeted by conspecifics.



There are limitations to our study which stem from the constraints inherent to purely observational protocols conducted in natural settings and the difficulty to control for a range of social and other environmental stimuli. Testing alternative social learning mechanisms in the field is more challenging than in the controlled laboratory conditions (van de Waal et al. 2010). However, future observational studies should investigate the effect of social facilitation, whereby the mere presence of conspecifics in the vicinity of the focal subject is sufficient to enhance its motivation (by disinhibition) to engage in any kind of activities and, particularly stressful, challenging and/or risky ones, such as RB (e.g. by systematically comparing RB rates in three conditions: absence of any conspecifics vs. presence of conspecifics but in the absence of any RB demonstration vs. presence of RB demonstrators). Social facilitation has been found to operate in many group-living species, especially in feeding contexts (Zentall 1996). Future field experimental research could also help to assess whether indirect social influence (e.g. stimulus enhancement, but in the absence of RB demonstrations) contributes to the learning and maintenance of RB-related behaviours in the Uluwatu macaques. Indeed, naive individuals may learn from encountering and manipulating specific RB behavioural artefacts present in their local environment, such as tokens discarded by conspecifics after unsuccessful bartering attempts. The daily performance and long-term persistence of another form of material culture in a closely related primate species (i.e. stone handling behaviour in free-ranging Japanese macaques, *M. fuscata*) is reliant on similar social influence, based on the physical traces (i.e. piles of stones) left behind by previous performers (Leca et al. 2010). Finally, through repeated and associative exposure to temple visitors, tokens, RB demonstrators, and the remains of food rewards (e.g. fruit peels, empty bags of crackers), the Uluwatu macaques could learn and maintain the RB practice via affordance learning or goal emulation, whereby the object affordances and the end product of an activity are learned, but the process (i.e. the correct sequence of actions) to reach that goal may vary (cf. Tomasello 1998; Whiten 2000). Although goal emulation is a plausible social influence candidate in the synchronous expression of RB-related behaviours, our protocol did not allow us to properly test whether the witness actually learnt about the goal of the demonstrator's actions or local environmental affordances. Future field experimental protocols comparing the exposition to different sequences of RB-related actions performed by demonstrators and a “ghost control” condition without any visible agent (Whiten 1998) could help to investigate this question.

Finally, our results do not point to a strong role of imitative processes in the performance of RB-related behaviours in the Uluwatu macaques. Whereas “production imitation” is typically defined as the delayed replication of a

learned sequence of actions, the short time window associated with the local co-occurrence of robbing events among multiple monkeys was more parsimoniously explained by response facilitation, defined as the rapid enhancement of a motor response triggered by exposure to a similar behaviour performed by conspecifics (Hoppitt et al. 2007; Kopp and Graeser 2006). “Contextual imitation” of RB was also unlikely (cf. Byrne 2002). Indeed, the data from the MCF condition indicated that even when the monkeys were placed in an environmental context similar to that of the WF, only without any RB demonstration, they did not tend to replicate similar RB-related behaviours beyond the period of exposition to a demonstration.

## Conclusion

In a previous study, we showed that robbing and bartering in the Uluwatu macaques was a population-specific behavioural practice, prevalent and persistent across multiple generations and characterized by marked intergroup variation (Brotcorne et al. 2017). In this study, we found that the synchronized expression of RB was socially influenced and more specifically explained by response facilitation. This result further supports the cultural nature of RB in this primate population. Future research steps will include field experiments to test the effect of alternative social and individual learning processes in the acquisition, performance, diffusion and maintenance of the RB behavioural tradition.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Human and animal rights statement** This research was exclusively observational and non-invasive, focusing on the spontaneous expression of behaviours by free-ranging macaques. The animals observed in the study were already habituated to human presence. This research protocol was approved by the Animal Welfare Committee of The University of Lethbridge (Protocol #1430), and adhered to the ASAB/ABS Guidelines for the use of Animal in Research. Our study was conducted with research permission from the Indonesian Ministry of Research and Technology (F.B.: #328/SIP/FRP/E5/Dit.KI/IX/2015; A.H.: #410/SIP/FRP/E5/Dit.KI/X/2015, L.J.-S.: #76/SIP/FRP/E5/ Dit.KI/XII/2015),

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