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Waiting for better, not for more: corvids respond to quality in two delay maintenance tasks

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Self-control, that is, overcoming impulsivity towards immediate gratification in favour of a greater but delayed reward, is seen as a valuable skill when making future-oriented decisions. Experimental studies in nonhuman primates revealed that individuals of some species are willing to tolerate delays of up to several minutes in order to gain food of a higher quantity or quality. Recently, birds (carrion crows, *Corvus corone*, common ravens, *Corvus corax*, Goffin cockatoos, *Cacatua goffiniana*) performed comparably to primates in an exchange task, contradicting previous notions that birds may lack any impulse control. However, performance differed strikingly with the currency of exchange: individuals of all three species performed better when asked to wait for a higher food quality, rather than quantity. Here, we built on this work and tested whether the apparent difference in levels of self-control expressed in quality versus quantity tasks reflects cognitive constraints or is merely due to methodological limitations. In addition to the exchange paradigm, we applied another established delay maintenance methodology: the accumulation task. In this latter task, food items accumulated to a maximum of four pieces, whereas in the exchange task, an initial item could be exchanged for a reward item after a certain time delay elapsed. In both tasks, birds (seven crows, five ravens) were asked to wait in order to optimize either the quality or the quantity of food. We found that corvids were willing to delay gratification when it led to a food reward of higher quality, but not when waiting was rewarded with a higher quantity, independent of the experimental paradigm. This study is the first to test crows and ravens with two different paradigms, the accumulation and the exchange of food, within the same experiment, allowing for fair comparisons between methods and species.

Animals regularly encounter choice situations in which the alternatives' values and consequences vary in time. Such intertemporal choice situations occur naturally in various contexts (Stevens & Stephens, 2010), ranging from foraging decisions (Kacelnik, 2003; reviewed in Stephens & Anderson, 2001) to social interactions, for example mate choice (Sozou & Seymour, 2003) or reciprocity in cooperative events (Stevens & Hauser, 2004). Going for the immediately available but less preferred option instead of postponing action in favour of an overall better but delayed reward is defined as impulsivity, whereas self-control refers to the opposite strategy (Ainslie, 1974; Kalenscher, Ohmann, & Güntürkün, 2006; Logue, Chavarro, Rachlin, & Reeder, 1988).

From an economical point of view, the preference for a maximum payoff should be selected for (Noë, Hooff, & Hammerstein, 2001); still, some nonhuman animals tested in self-control set-ups commonly favour the immediate option, even when the delayed one results in a reward of higher value (e.g. pigeons, *Columba livia*: Ainslie, 1974; common marmosets, *Callithrix jacchus*, and cottontop tamarins, *Saguinus oedipus*: Stevens, Hallinan, & Hauser, 2005; domestic fowl, *Gallus gallus domesticus*: Abeyesinghe, Nicol, Hartnell, & Wathes, 2005). It has been commonly suggested that temporal discounting is a critical factor in intertemporal decisions (Kacelnik & Bateson, 1996; Kalenscher & Pennartz, 2008; Stevens & Stephens, 2010). Accordingly, future rewards are subjectively rated less valuable the longer the delay until they are received, because delay is associated with uncertainty for realization of the benefits and probability of loss. Alternatively, it has been argued that choosing an immediate option may be appropriate in relation to reproduction (Sozou & Seymour, 2003). Furthermore, impulsive foraging actually leads to maximized long-term rates of food intake (Kagel, Greent, & Caraco, 1986; Stephens, 2002; Stephens & Anderson, 2001; Stephens, Kerr, & Fernández-

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Juricic, 2004). It is difficult to ascertain whether impulsiveness is an adaptive strategy, or rather a cognitive constraint, since the optimal model of choice may depend on the particular situation (Fawcett, McNamara, & Houston, 2012; Stevens & Stephens, 2010).

From a cognitive point of view, the ability to delay gratification is seen as a critical skill for making future-oriented decisions in various contexts (e.g.: Kacelnik, 2003; Mischel, 1974). In humans, the degree of impulse control varies markedly between individuals (Mischel, Shoda, & Rodriguez, 1989; Steelandt, Thierry, Broihanne, & Dufour, 2012), particularly depending on the social conditions during early upbringing (Diamond & Lee, 2011). Impulse control is a core competence of 'executive functions' (Miyake et al., 2000), which strongly predicts individual academic success and involvement in society. In mammals, these 'executive functions' are associated with the prefrontal cortex (Miyake et al., 2000). The corresponding avian forebrain structure, the nidopallium caudolaterale, is highly similar in terms of anatomy, neurophysiology and cognitive characteristics (Güntürkün, 2005). In birds, food-storing behaviour offers an illustrative example of how future anticipation and the need to plan for the future may have reinforced the evolution of self-control (Feeney, Roberts, & Sherry, 2011; Raby, Alexis, Dickinson, & Clayton, 2007).

The operational level of self-control and the ability to delay gratification has been investigated by applying tasks in which subjects are given the choice either to take an immediately available but smaller or less-preferred food item, or to wait for a larger or more preferred food reward. In so-called delay choice tasks, subjects cannot modify their decision once a choice has been made, whereas in delay maintenance tasks, subjects are allowed to discontinue waiting at any point. A drawback of delay choice tasks is that the choice for the better, usually larger, delayed option is effected by an impulsive tendency to point to the larger food, and the task does not test whether the subject is able to sustain the chosen delay (for discussion see Bramlett, Perdue, Evans, & Beran, 2012; Paglieri et al., 2013). Common delay maintenance tasks make use of the exchange or the accumulation paradigm. In exchange tasks, subjects can return an initial item after a certain delay in order to obtain a reward of higher value (in terms of either quality or quantity), or consume the item at any time during the delay. In accumulation tasks, subjects can maximize the gain of sequentially delivered food items, or stop the accumulation by consuming the food.

Surprisingly few attempts have been made to reconcile different approaches and apply different experimental procedures within the same study, although recent studies on capuchin monkeys, *Cebus apella*, have compared performance in a delay choice and in a delay maintenance task (Addessi et al., 2013), and used a novel methodology, the hybrid delay task, to assess the ability to maintain a chosen delay (Paglieri et al., 2013). In fact, animals sustain varying delay times, depending on the experimental approach (outlined in Pelé, Micheletta, Uhlrich, Thierry, & Dufour, 2011). This may have various reasons; for example, some tasks require particular training, whereas others aim at an intuitive understanding of the task (Bramlett et al., 2012). Importantly, tasks also differ in respect to what happens during the waiting period. In the accumulation task, the reward constantly increases in value over time (e.g. Evans & Beran, 2007), whereas in the exchange task, the reward remains the same throughout the delay (e.g. Pelé, Dufour, Micheletta, & Thierry, 2010). Accordingly, the impulsive option may become a stronger temptation in the accumulation than in the exchange task. Yet, the exchange procedure appears to be more complex than the accumulation task, as subjects not only have to suppress impulses for immediate food consumption in favour of profitability but additional cognitive skills may also be required to judge and compare the trade values (Drapier, Chauvin, Dufour, Uhlrich, & Thierry, 2005). Another critical aspect in applying the exchange task is that not all nonhuman animals have functional hands but, as is the case in birds or dogs, have to keep the initial item in their beak or mouth; having the food already in the oral cavity could potentially make it more difficult to control the impulse to eat the initial item (Leonardi, Vick, & Dufour, 2012; Wascher, Dufour, & Bugnyar, 2012).

Both paradigms have been applied to various primate species, revealing waiting performances from some seconds up to several minutes (e.g. exchange task: chimpanzees, *Pan troglodytes*: Dufour, Pelé, Sterck, & Thierry, 2007; capuchin monkeys: Drapier et al., 2005; accumulation task: bonobos, *Pan paniscus*: Stevens, Rosati, Heilbronner, & Mühlhoff, 2011; capuchin monkeys and squirrel monkeys, *Saimiri sciureus*: Anderson, Kuroshima, & Fujita, 2010; chimpanzees and orang-utan, *Pongo pygmaeus*: Beran, 2002; Beran & Evans, 2009; rhesus macaques, *Macaca mulatta*: Evans & Beran, 2007; both paradigms: longtailed macaques, *Macaca fascicularis*: Pelé et al., 2010; Tonkean macaques, *Macaca tonkeana*, and capuchin monkeys: Pelé et al., 2011). The exchange paradigm has recently been applied in two corvid species, the common raven, *Corvus corax*, and the carrion crow, *Corvus corone*, and one parrot species, the Goffin cockatoo, *Cacatua goffiniana*. The tested species performed well, in a manner comparable to primates, in overcoming impulsivity in order to optimize food quality, but were considerably worse than primates in the context of quantity (Auersperg, Laumer, & Bugnyar, 2013; Dufour, Wascher, Braun, Miller, & Bugnyar, 2012; Wascher et al., 2012). The only avian species that has been tested for self-control with the accumulation paradigm performed rather impulsively, waiting only a few seconds for larger rewards (African grey parrots, *Psittacus erithacus*: Vick, Bovet, & Anderson, 2010).

We investigated whether avian performances in previous experiments were predisposed by the methodological paradigm and, for the first time in birds, applied the accumulation and the exchange paradigm within the same experiment. We expected individuals to perform similarly in both tasks, suggesting that specific cognitive abilities may account for the high level of impulse control in crows and ravens, relative to other bird species. Alternatively, differing results between the tasks would point towards a methodological bias in previous studies on birds.

Additionally, we ran modifications of the original exchange task (Dufour et al., 2012; Wascher et al., 2012), which allowed us to explore the effects of differing relative attractiveness of the initial item and the potential reward. In exchange trials, we presented the subjects with various combinations of food items that differed in quality, whereas in previous studies, subjects were only asked to exchange food of low quality for higher, that is, the initial item was always a less-preferred food item. Birds were expected to be less likely to exchange when the initial item, the food to be returned, was of similar quality to the subsequent reward (as found in capuchin monkeys: Drapier et al., 2005), or when the possible reward was of relatively low value. Finally, we aimed to investigate whether self-control in crows and ravens is mediated by the 'value' of food. Specifically, we tested the assumption that the ability to maintain a delay in order to get a greater amount of food depends on the subjective preference of the food, with less-preferred food being easier to restrain from immediate consumption.

METHODS

Ethical Note

Individuals participating in the experiments were all hand-raised and either zoo-bred (three ravens), picked up by private people as apparently injured or abandoned young (all crows, one