OBJECT PERMANENCE IN THE RACCOON (*PROCYON LOTOR*)

JENNIFER A. COLBOURNE

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Abstract

Two studies are conducted to test object permanence in infant and adult raccoons. The raccoon (*Procyon lotor*) is an omnivorous generalist known for its primate-like intelligence, but has never been given object permanence testing. In Study 1, infant raccoons (kits) of 12 and 16 weeks failed single visible displacement tasks conducted with either two or three cups as hiding places. Therefore, unlike other carnivores that have been tested, raccoon kits do not appear to have developed Stage V object permanence by the age of weaning or age of independence from the mother. Adult raccoons in Study 2 performed above chance on single visible displacements, but did not pass multiple visible displacements, invisible displacements, transpositions and rotations. These results suggest that the raccoon is limited to representing visible displacements, and is therefore a Stage V species.

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Introduction

Object permanence, the understanding that an object continues to exist when it cannot be seen, has traditionally been an important measure of cognition in both developmental and comparative psychology. The concept was introduced by Jean Piaget (1937/1954), who delineated its development into six discrete stages based on detailed observations of his three children as infants. According to Piaget, at birth the world contains no objects; at Stages I-II the infant can being to recognize images, but they are not spatially organized or substantially permanent. The child's universe begins to solidify in Stage III, and the child can find partially hidden objects; however, if the object is completely covered, it is as if it has disappeared. At Stage IV, the child learns to actively search for hidden objects, but with one caveat: the first place ("A") the object is found takes on a special status, and when the object is subsequently hidden in another place ("B"), the child still searches this initial location; Piaget (1937/1954) labelled this Stage IV behaviour as "the typical reaction" (p. 50), although later it would be more commonly referred to by other researchers as "the A-not-B error" or "the perseverative error." When the child no longer searches for an object in a privileged position, but instead the location of the last displacement (single visible displacement, or SVD), they are considered to have entered Stage V. If an object is hidden in one location, then visibly removed and hidden in another location, the child will correctly search the last location in the sequence (multiple visible displacement, or MVD). However, if a desired object is put in a container, the container is deposited behind a cover and the object invisibly removed, and then the container is brought out and shown to be empty (single invisible displacement, or SID), the child does not understand that the object must have been left behind the cover. The child cannot account for invisible displacements (IDs); their search only takes into consideration displacements they have actually seen (visible displacements, or VDs). The final stage, Stage VI, is attained when the child can represent these unobserved displacements, including sequences of invisible displacements under multiple covers (multiple invisible displacement, or MID). Now the object is considered to be substantial and fully independent from the child's actions and perceptions, obeying spatial and kinematic laws. By achieving full object permanence, the child can successfully organize causality, space, and time. Furthermore, according to Piaget (1937/1954), the ability to fully represent unseen objects forms the foundation for future symbolic and conceptual thinking.

Abbreviation	**Task**	**Stage**	**Description**
SVD	Single Visible Displacement	Va	Object is hidden behind one of several screens.
MVD	Multiple Visible Displacement	Vb	Object is hidden behind one screen, then visibly removed and hidden behind another screen.
SID	Single Invisible Displacement	VIa	Object is hidden in a container, then hidden behind one of several screens, and then the container is shown empty.
MID	Multiple Invisible Displacement	VIb	Object is hidden in a container, then the container is hidden behind one screen, then removed and hidden behind another screen and the object secreted, and then the container is shown empty.

Table 1. Piagetian task terminology.

Object Permanence Testing in Humans

In 1975, Užgiris & Hunt created *Assessment in Infancy: Ordinal Scales of Psychological Development* as an instrument for researchers to assess infants' development according to Piaget's sensorimotor theory. The scales essentially codified the activities Piaget (1937/1954) gave his children as formal tests, changing very little about the methodology. Two more measures of IDs were later introduced as common test measures: transposition problems, in which a reward is hidden in a container and swaps position with another container (Sophian & Sage, 1983), and rotations, in which the containers are placed on a platform then rotated (Bremner, 1978). Unlike traditional Piagetian ID tests, in which almost all participants could solve MIDs at 2 years (Sophian & Sage, 1983), transpositions were not consistently solved by all participants until at least 6 years (Sophian, 1986) and rotations until 7 years (Lasky, Romano & Wenters, 1980). Barth & Call (2006) have suggested that rotations are the most difficult task because of the number of elements changing places – platform, containers, and reward – whereas in transpositions only two elements change, and in IDs only one (the reward). Whether rotations and transpositions can be considered "true" object permanence tests, though, is debatable (Beran & Minihan, 2000). These tasks require the subject to attend to the movements of relevant containers, but do not necessarily require the belief that object hidden within still exists; this makes it necessary to give traditional Piagetian object permanence tasks in conjunction with these transposition and rotation tests (Beran & Minihan, 2000).

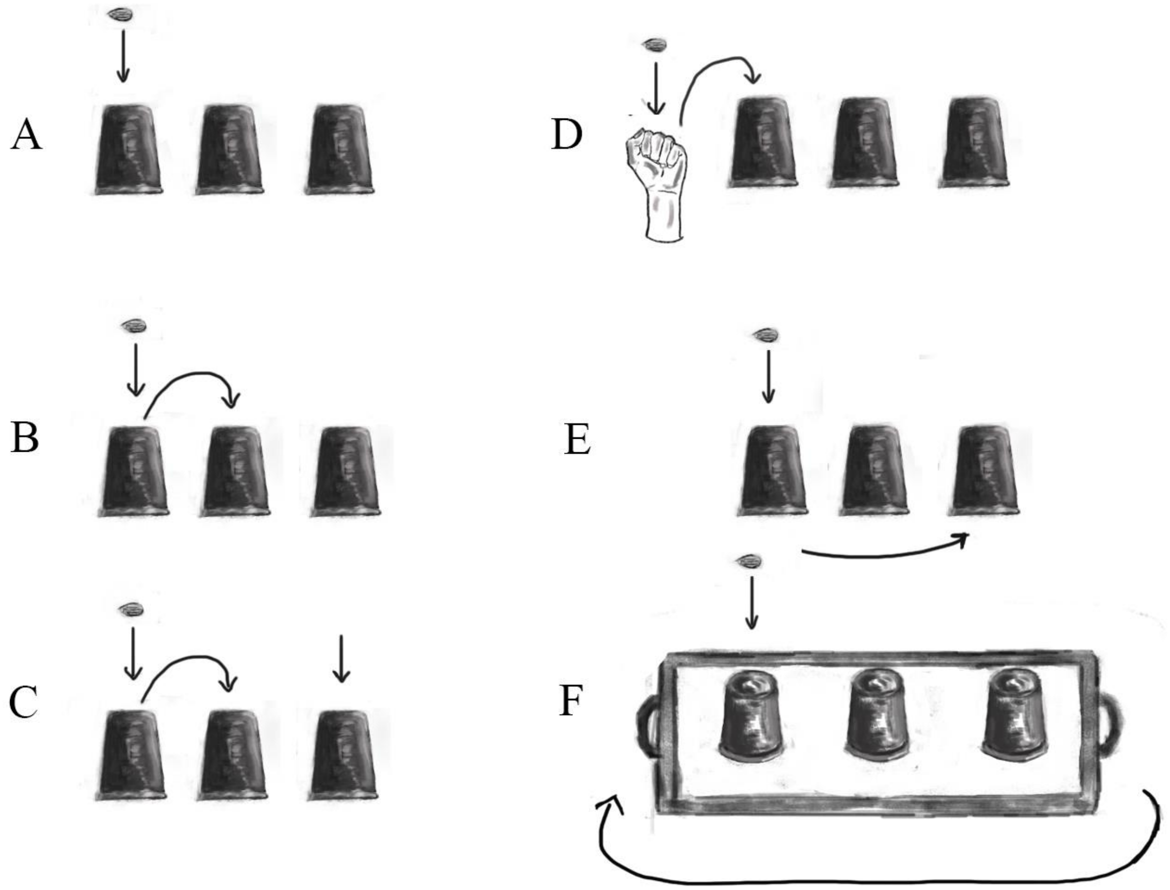

Figure 1. Illustrations of each OP test. A: Single Visible Displacement (SVD); B: Multiple Visible Displacement (MVD); C: MVD control; D: Single Invisible Displacement (SID); E: Transposition; F: Rotation

Object Permanence Testing in Nonhuman Animals

Comparative research in object permanence (OP) began with an interest in whether Piaget's (1937/1954) stages developed in the same order in other species, and at what pace (Gruber, Girgus & Banuazizi; Mathieu, Brouchard, Granger & Herscovitch, 1976; Parker, 1977; Wise, Wise & Zimmermann, 1974; Wood, Moriarty, Gardner & Gardner, 1980). It became rapidly clear that OP developed far faster in nonhuman species with the exception of chimpanzees, which developed at a similar timeline as children (Wood et al., 1980). However, as new tests were developed with more rigorous controls, doubt was cast on whether any species besides great apes could reach Stage VI. With Piaget's (1937/1954) contention that Stage VI representation was necessary for symbolic communication, new interest was taken in OP testing within comparative psychology, with some researchers hypothesizing that there is a cognitive divide between monkeys and great apes (de Blois & Novak, 1994, 1998; Natale et al., 1986). Therefore, any species that can reach Stage VI is considered to be uniquely intelligent. On the other hand, species that cannot reach Stage IV or Va are notable as well, because this means that they do not even have a rudimentary understanding that objects can disappear, which puts a severe limit on their capability to track, hunt and forage. This is informative for cognitive testing, as subjects that have not yet developed basic OP cannot be tested with standard equipment such as a Wisconsin General Apparatus (Vaughter, Smotherman & Ordy, 1972). Comparative OP research has thus become an indicator of a species' intelligence, at least in the area of visual representation and conceptual thinking.

Nonhuman primates.

Early object permanence testing of Old World and New World monkeys revealed that monkeys' OP progression followed the chronology of the Užgiris & Hunt (1975) scale, and that mature monkeys could pass all of the Piagetian stages (Mathieu et al., 1976; Parker, 1977; Vaughter et al., 1972; Wise et al., 1974). These results would later be questioned because they were based on a large number of trials for each subject, which may have enabled trial-and-error learning of task specific cues rather than true OP comprehension (de Blois & Novak, 1994; de Blois, Novak & Bond, 1998; Dumas & Brunet, 1994; Natale 1989). Furthermore, as tests were given in order of difficulty, there could be learning over tests; for instance, a SID with only one container could be solved simply because the subject had already learned to associate containers with rewards (Doré, 1986; Dumas & Brunet, 1994; Gagnon & Doré, 1992). Even more concerning, Fischer & Jennings (1981) argued that several of Užgiris & Hunt's (1975) tests could be solved using the practical strategy of selecting whichever container had been touched last by the experimenter. Natale, Antinucci, Spinozzi & Potì (1986) tested this idea with a 22-month-old Japanese macaque (*Macaca fuscata*) and 22-month-old lowland gorilla (*Gorilla gorilla*) that had previously given evidence of attaining Stage V object permanence (Antinucci, Spinozzi & Natale, 1986; Potì, 1983). Using the standard version of the SID task, the Japanese macaque performed above chance. However, when the subject was given "false" trials in which the reward was not displaced behind either container, but one of the empty containers was lifted by the experimenter, the macaque's performance fell to chance levels, indicating that it had been relying on the practical rule of selecting the last container touched. The macaque was then given 130 more trials to see if it could be taught to respond correctly to the false trials, and by the last two sessions the subject made only a few errors. The test was then modified again to have "nonlinear" trials in which the displacer (the container used to displace the reward) was placed next to the unrewarded container. While the Japanese macaque only made one error on linear trials, it made 29/43 errors on the nonlinear trials, revealing that it had adopted the new practical strategy of selecting whichever container was adjacent to the displacer. The gorilla made no such errors. According to Natale et al. (1986), these results indicate that macaques, unlike great apes, are confined to Stage V and do not truly represent hidden objects. Further testing by subsequent researchers has confirmed these findings in various monkey species (rhesus monkeys (*Macaca mulatta*), de Blois & Novak, 1994; squirrel monkeys (*Saimiri sciureus*), de Blois et al., 1998; Japanese macaques, Natale, 1989; crab-eating macaques (*Macaca fascicularis*), Natale, 1989; Schino, Spinozzi & Berlinguer, 1990; tufted capuchins (*Cebus apella*), Dumas & Brunet, 1994; Natale, 1989; Schino, Spinozzi & Berlinguer, 1990).

Only one tufted capuchin is claimed to have passed all control tests (Schino et al., 1990), but no other tufted capuchins have shown this ability. In 2003, Neiworth, Steinmark, Baisle, Wonders, Steely & DeHart argued that cotton top tamarins (*Saguinius oedipus*) had some capacity for representing IDs because they could pass SIDs, though they failed control tasks for MIDs. Neiworth et al. (2003) did not address the possibility that the tamarins could have passed the SIDs by selecting the only container manipulated by the experimenter, and other researchers have not been convinced that the tamarins succeeded beyond Stage V (Barth & Call, 2006; Fedor, Skollár & Ujhelyi, 2008; Jaakkola, 2014). Mendes & Huber (2004) claimed that two of their eleven common marmoset (*Callithrix jacchus*) subjects could pass MIDs, including control trials; however, they have been criticized for not reporting the two successful subjects' individual error rates, making it unclear whether they were actually using a strategy to pass MIDs (Jaakkola, 2014). If monkeys have some limited capacity for Stage VI representation, it is clearly an upper limit reached by few exceptional individuals[1].

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[1] Filion, Washburn & Gulledge (1996) have given convincing evidence that rhesus monkeys can represent unseen objects as they move behind an occluder, which indicates that they may have a capacity for prospective processing of IDS, but not retrospective processing as tested by traditional Piagetian OP tasks.

Great apes, on the other hand, have clearly demonstrated their OP abilities. Chimpanzees (*Pan troglodtyes*), bonobos (*Pan paniscus)*, orangutans (*Pongo pygmaeus*) and gorillas have all been found to pass all VDs and IDs above chance without using practical strategies, although VDs are consistently found to be easier than IDs (Barth & Call, 2006; Beran & Minihan, 2000; de Blois et al., 1998; Call, 2001; Hallock & Worobey, 1984; Mathieu et al., 1976; Mathieu & Bergeron, 1981; Natale et al., 1986; Redshaw, 1978; Wood et al., 1980). Great apes have performed very well on non-traditional OP tasks, such as transpositions and rotations (Albiach-Serrano, Call & Barth , 2010; Barth & Call, 2006; Beran & Minihan, 2000; Call, 2003; Rooijakkers, Kaminski & Call, 2009). Barth & Call (2006) found that, like the children they tested, rotations were the most difficult task, transpositions the next difficult and traditional Piagetian OP tasks easiest for the great apes. Some great apes have even shown the ability to track embedded representations of objects in which the container is not visually baited, but temporarily marked with a symbol associated with a food reward (Beran, Beran & Menzel, 2005; Call, 2003; but see Okamoto-Barth & Call, 2008). Computer-trained apes have also succeeded on digital versions of VDs and rotations, including four boxes moving simultaneously multiple positions (Beran & Minihan, 2000). Although all of the great ape species perform above chance on OP tasks, chimpanzees and bonobos appear to slightly outperform gorillas and orangutans (Albiach-Serrano et al., 2010; Barth & Call, 2006).

Smaller apes perform more like monkeys than great apes, reaching only Stage V on the traditional OP tasks (Anderson, 2012; Fedor et al., 2008), although some of siamangs (*Symphalangus syndactylus*) and Northern white-cheeked gibbons (*Nomascus leucogenys*) have performed above chance on transpositions (Anderson, 2012). Although prosimians can pass MVDs, they perform far worse than monkeys, and cannot delay more than 5 s on an SVD without forgetting an object has been hidden (Deppe, Wright & Szelistowski, 2009). However, Mallavarapu, Perdue, Stoinski & Maple (2013) found that black-and-white ruffed lemurs (*Varecia variegata*) could not pass MVDs when controlling for practical strategies, and they have called into question whether prosimians have a true understanding of even basic VDs.

Carnivores.

The very first OP test of a nonhuman animal was conducted by Gruber et al. (1971) with cats (*Felis catus*). They found kittens would not uncover a hidden toy until 16 weeks of age, but they did not test MVDs or IDs, assuming that the cats would fail. Other researchers disagreed with Gruber et al. (1971), arguing that cats would need to be able to track an object in several hiding places in order to hunt (Thinus-Blanc, Poucet & Chapuis, 1982; Triana & Pasnak, 1981). Thinus-Blanc et al. (1982) discovered that cats performed above chance level on MVDs, while Triana & Pasnak (1981) found that cats could succeed on IDs as well, given sufficient motivation (a food reward instead of a toy).

Doré (1986) challenged Triana & Pasnak's (1981) findings. While Doré (1986) also found that cats could pass various VDs, his subjects failed IDs. According to Doré (1986), Triana & Pasnak (1981) had flawed methodology because there was only one container used for the ID; consequently, cats that had experience with VDs could have learned to associate containers with rewards, and so searched the only available hiding place. Doré (1986) found that cats that had no prior experience with VDs failed the ID tasks, findings which were replicated by Pasnak, Kurkjian & Triana (1988) and again by Doré (1990). Thus cats appear to be Stage V organisms.

Interestingly, a longitudinal study of OP development in kittens discovered that kittens passed all various VDs in one developmental step at the age of 48 days, with no sign of the A-not-B error (Dumas & Doré, 1989).[2] Their performance did not differ from 150-day-olds, indicating that Stage V OP was fully developed at 48 days. Notably, this is also the time the mother cat begins to teach her kittens how to hunt. Similarly, puppies were found to succeed on all VDs at 56 days, and performed just as well as 84-day-old puppies (Gagnon & Doré, 1994). Thus, like cats, full development of Stage V appears to coincide with the weaning period, suggesting that weaning is an important developmental milestone for cognition (Gagnon & Doré, 1994). The early and full development of VD in puppies and kittens is suggested to occur because they are mobile at birth, allowing the development of an "early allocentric spatial code" (Dumas & Doré, 1989, p. 199; Gagnon & Doré, 1994).

Although it was firmly established that cats could not solve traditional Piagetian IDs, Dumas (1992) began to question whether cats failed simply because the tests were ecologically irrelevant for cats with their use of a displacer. In response, Goulet, Doré & Rousseau (1994) designed two experiments in which no containers were used, with movable panels indicating where the reward was located. In SIDs, when the reward was invisibly moved to the second container, the panel was lifted to reveal the reward's new location. Even with additional indications that the reward had been displaced, including lifting the panel to show that the first container visited was now empty, the cats still performed very poorly, searching equally at both locations. Goulet et al. (1994) concluded that cats could only represent directly perceived changes in location. They hypothesized that if an object has not appeared to have moved, both locations may be activated in working memory, even if there are other cues indicating the object has been transferred (Goulet et al., 1994). Therefore, activation of working memory relies on an

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[2] The A-not-B error is a robust phenomenon in humans (Wellman, Cross & Barsch, 1986) and has been documented as occurring in several infant primates (Natale, 1989; Parker, 1977; Potì, 1989; Wise et al., 1974).

object’s visible disappearance behind a location, and deactivation relies on its visible removal, findings which were subsequently replicated by Goulet, Doré & Lehotkay (1996).

For many years it was assumed that dogs (*Canis familiaris*) could pass both SIDs and MIDs. Dogs without prior VD experience were found, unlike cats, to pass IDs, though they performed better with prior VD experience (Gagnon & Doré, 1992; Pasnak et al., 1988; Triana & Pasnak, 1981), making them unlike primates, which do not show such improvement (Barth & Call, 2006; de Blois & Novak, 1994; de Blois et al. 1998; Fedor et al., 2008). Although dogs showed significantly more olfactory responses when solving IDs compared to VDs, trials controlling for odour cues revealed that dogs were not using olfaction to solve IDs (Gagnon & Doré, 1992). Breed differences were also not a significant factor (Gagnon & Doré, 1992). Despite failing to employ controls, Gagnon & Doré (1992, 1993) were certain that dogs were not using a practical strategy because the dogs’ performance did not improve over trials, and there was no evidence that they were systematically choosing the last container visited.

However, dogs were found to fail transposition tasks, performing similarly to cats (Doré, Fiset, Goulet, Dumas & Gagnon, 1996). Coupled with their poor performance on IDs, Doré & Goulet (1998) admitted that it was unlikely dogs were a true Stage VI species. A clever experiment by Watson, Gergely, Csányi, Topál, Gácsi & Sárközi (2001) further established that dogs did not understand the inferential element of IDs, as they did not appear to realize in MIDs that an empty container increased the likelihood that the reward was in the next container. The dogs in Watson et al.’s (2001) study also consistently began by searching the last container visited by the experimenter, indicating that they do use practical strategies with IDs.

This possibility was thoroughly investigated by Collier-Baker, Davis & Suddendorf (2004) who followed Natale et al.’s (1986) controls for last container visited by the displacer, and container adjacent to the displacer. Additionally, they introduced more rigorous controls for experimenter cues. They successfully ruled out that dogs were using a last container visited or first container visited strategy, or experimenter cueing. However, they did find that the dogs were using the strategy of selecting whichever container was adjacent to the displacer. When the displacer was removed from the array, dogs performed at chance level, and on 43% of trials refused to even search (compared to only 10% of standard trials) (Collier-Baker et al., 2004, p. 429). Like Gagnon & Doré (1992, 1993), they did not see any gradual improvement over trials that would indicate learning effects; therefore, the association with the displacer that formed the basis of their practical strategy was spontaneous. Unlike dogs, 24-month-old children given the same displacer control task performed above chance (Collier-Baker et al., 2004), as did chimpanzees in a second study (Collier-Baker & Suddendorf, 2006). The results with dogs were replicated by Fiset & LeBlanc (2007), who further found that the dogs will use the experimenter as a landmark.

Rooijakkers et al. (2009) suggested that it was possible that dogs had lost the ability to represent IDs in the process of domestication. Fiset & Plourde (2013) tested this hypothesis by giving wolves (*Canis lupus*) and dogs both VDs and transposition tests. Both species were equally successful on SVDs and MVDs, and equally unsuccessful on transpositions. Fiset & Plourde (2013) concluded that dogs and wolves are dependent on an “action/reaction strategy” when looking for disappearing objects, and argued that wolves don’t actually need to represent each member of the pack when hunting (p. 124).

Research with bears has begun only recently. Sloth bears (*Melursus ursinus ursinus*) and sun bears (*Helarctos malayanus euryspilus*) have both been found to succeed above chance in SVDs (Amici, Cacchione & Bueno-Guerra, 2017; Hartmann, Davila-Ross, Wong, Call &

Scheumann, 2017), although a delayed reaction experiment with sloth bears found that they could not recall an object's hidden location after 30+ s (Amici et al., 2017). This is very different from dogs, who can recall locations with great accuracy after 240+ s (Fiset, Gagnon & Landry, 2003). However, unlike dogs, sloth bears were found to succeed above chance on transpositions, though all the sun bears except one failed.[3] No improvement was found between first and last sessions, indicating that the sloth bears were not learning. A variety of control trials revealed that the sloth bears were not using audition, olfaction or practical strategies to succeed either. Bear OP is thus a promising avenue for future research to see what other Stage VI tasks are within the capacity of different bear species.

Other animals.

Very few mammals other than primates or carnivores have been tested to date. Golden hamsters (*Mesocricetus auratus*) (Thinus-Blanc & Scardigli, 1981), swine (*Sus scrofa*) (Albiach-Serrano, Brauer, Cacchione, Zickert & Amici, 2012) and dwarf goats (*Capra aegagrus hircus*) (Nawroth, von Borell & Langbein, 2015) have all passed SVD tasks, and while swine have failed transpositions, dwarf goats have passed, although with poor controls and a performance suggesting the use of a combination of simple strategies (Nawroth et al., 2015).

Dolphins (*Tursiops truncatus*) have been considered a promising candidate for Stage VI object permanence due to their advanced cognitive abilities, but to date they have only passed Piagetian VDs and none of the ID tests (Doré, Goulet & Herman, 1991, as cited by Doré & Goulet, 1998; Jaakkola, Guarino, Rodrigues, Erb & Trone, 2010). However, a visual tracking task has indicated that dolphins are capable of tracking unseen objects and inferring their transfer

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[3] Hartmann et al. (2017) warn about making any assumptions about species differences based on the success of the sloth bears and failure of the sun bears in their study, as the sun bears were rescues with likely abnormal rearing and development in their youth.

to another location (Johnson, Sullivan, Buck, Trexel & Scarpuzzi, 2015). It may be that traditional Piagian OP tasks are inherently unsuited to a species that lives underwater (Jaakkola et al., 2010; Johnson et al., 2015).

The only animal that does not appear to achieve basic object permanence is the common pigeon (*Columba livia*), unable to even be operant conditioned to respond to a disappearing object (Plowright, Reid & Kilian, 1998). Their close relative, the ring dove (*Streptopelia risoria*), cannot pass beyond Stage IV (Dumas & Wilkie, 1995) nor can tit species (*Paridae* spp) (Marhounová, Frynta, Fuchs & Landová, 2017). Chickens (*Gallus gallus domesticus*) (Etienne, 1973; Regolin, Rugani, Pagni & Vallortigara, 2005) and mynahs (*Gracula religiosa*) (Plowright et al., 1998) fare a little better, reaching Stage Va. Numerous corvid and parrot species, on the other hand, have succeeded on all tests of the Užgiris & Hunt (1975) scale, suggesting that these species, like great apes, have reached Stage VI.[4] However, use of the Užgiris & Hunt (1975) scale has come under intense criticism by Jaakkola (2014), since it lacks controls for practical strategies, and, as the tests are given in order of difficulty, allows for learning over trials. However, a promising new study by Auersperg, Szabo, von Bayern & Bugnyar (2014) with Goffin cockatoos (*Cacatua goffini*) that followed the methodological controls of de Blois & Novak (1994, 1998) found that the parrots succeeded on MIDs, transpositions and rotations.

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[4] Parrot species reaching Stage VI include African grey parrots (*Psittacus erithacus*) (Pepperberg & Kozak, 1986; Pepperberg & Funk, 1990; Pepperberg, Willner & Gravits, 1997), kakariki parakeets (*Cyanoramphus auriceps*) (Funk, 1996), an Illiger's macaw (*Ara maracana*) and a cockatiel (*Nymphicus hollandicus*) (Pepperberg & Funk, 1990). Corvid species reaching Stage VI include magpies (*Pica pica*) (Pollok, Prior & Güntürkün, 2000), ravens (*Corvus corax*) (Bugnyar, Stöwe & Heinrich, 2007), Eurasian jays (*Garrulus glandarius*) (Zucca, Milos & Vallortigara, 2007), carrion crows (*Corvus corone*) (Hoffmann, Rüttler & Nieder, 2011), and jackdaws (*Corvus monedula*) (Ujfalussy, Miklósi & Bugnyar, 2013).

Species of Investigation

No OP testing has ever occurred with the common raccoon (*Procyon lotor*). However, raccoons were tested in a delayed reaction experiment by Hunter (1913), who also tested rats (*Rattus norvegicus*), dogs, and human children. The delayed reaction task shares several similarities with SVDs. In a delayed reaction experiment, a light, which the subject has been conditioned to associate with food, flashes in one of three arms in a maze. The subject is then released, and if it selects the previously lighted arm, it receives a reward. Then the subject is restrained for increasing amounts of time to see how long it can remember which arm is correct. The rats in the study could only typically delay for a few seconds, whereas the raccoons could delay up to 25 seconds and the dogs up to 5 minutes. However, while it was found that the rats and dogs depended on head or body orientation to maintain their memory, the raccoons could delay correctly with no such strategies, performing well even when the experimenter distracted them by yelling at them loudly. Hunter (1913) concluded that the raccoons he tested were using some kind of internal cues, which he deemed “sensory thought” or “imageless thought” (p. 81). He categorized the raccoons’ abilities as comparable to that of the 2.5-year-old child he tested (Hunter, 1913).

Other reports indicate at least rudimentary OP abilities in raccoons. Cole (1907) reported that a 9-week-old raccoon could recognize his bottle after seeing only the nipple, an account which closely parallels Piaget’s (1937/1954) own description of his infant Laurent’s progress with a bottle in Stage III, which involves learning to construct an “invisible whole from a visible fraction” (p. 27). In order to reach an apple that they had seen placed within a box, Cole’s (1907) raccoons found an alternate previously unused route inside as though they “retained an image of 'apple-there'" (p. 255).[5] McDougall & McDougall (1931) found that their leashed raccoon could turn around facing away from an object in order to reach it with its back foot, which they argued demonstrated that the raccoon had "imagination," since it could no longer perceive the object in its visual field (p. 260). Furthermore, raccoons are incredibly object oriented. An experiment by Thackray & Michels (1958) determined that raccoons could be trained on a T-maze with objects that they could manipulate as the sole reward. In the case of another experiment, the food reward actually had to be replaced with toys to maintain the subjects' interest (Davis, 1984). Raccoons can discriminate between objects of different colours[6] (Cole, 1907; Davis, 1907), geometric shapes (Cole, 1907; Fields, 1936), materials (Shell & Riopelle, 1957), sizes (Johnson & Michels, 1958b) and in numbers up to three (Davis, 1984).

Although seldom used as an experimental animal,[7] the few tests conducted with raccoons have revealed some primate-like cognitive abilities. Raccoons have learned to rapidly undo various complex combinations of fastenings (Cole, 1907; Davis, 1907), quickly form learning sets (Johnson & Michels, 1958b; Shell & Riopelle, 1957), solve crossed string problems (Michels, Pustek & Johnson, 1961), and use insight to remove obstructions (McDougall & McDougall, 1931) with a performance comparable to the monkeys also tested. Moreover,

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[5] Hunter (1913) argued that the raccoons could likely smell the apple inside, and rather than finding an alternate route were simply attracted to box openings; Cole (1915) directly responded, arguing that he had adequately controlled for apple scents.

[6] It has been convincingly argued that raccoons are colour blind (Gregg, Jamison, Wilkie & Radinsky, 1929; Munn 1930), or at least colour deficient (Zeveloff, 2002). However, they can still discriminate colours very successfully, though it may be based solely on brightness.

[7] According to Pettit (2010), this historic oversight is due not only to the difficulty of maintaining raccoons in a laboratory, but because the raccoon challenged reigning behaviorist orthodoxy with their unusual behaviors. For example, Skinner's former students Breland & Breland (1961) found it impossible to condition the raccoons in their amusement park to deposit coins in a box; the raccoons instead were compelled to rub them together and dip them in the box, leading Breland & Breland (1961) to argue that instinct has a definite role in behaviour.

raccoons have an extraordinarily long memory for remembering how to undo puzzles, with records of up to hundreds of days (Cole, 1907; Davis, 1907), can successfully learn reversals (Warren & Warren, 1962), and can learn from being put through an act (Cole, 1907). Still, raccoons are not quite as proficient at learning as monkeys. They do not imitate, or even pay attention to each other (Cole, 1907; Shepherd, 1911); nor were they found to be able to master double alternation (the pattern LLRRLLRR), learning only to change their response on the third trial like cats and dogs (Hunter, 1928; Johnson, 1961). A recent "Aesop's fable" study, in which the raccoons learned to drop stones in a tube in order to increase the water's height so that they could reach floating marshmallows, revealed that the raccoons did not have a causal understanding of the task, although the subjects still managed to find three novel and unintended ways to obtain the reward (Stanton, Davis, Johnson, Gilbert & Benson-Amram, 2017), an example of their unusual determination and resourcefulness.

The raccoon is an arboreal species, which a number of researchers have posited influenced the evolution of primate intelligence (Johnson & Michels, 1958), and has primate-like neuronal density in its cerebral cortex (Jardim-Messeder et al., 2017). On the other hand, unlike most primates, raccoons do not live in complex social groups, although unrelated male raccoons do form stable small bands and share territories (Gehrt & Fritzell, 1997; Gehrt & Fritzell, 1998b; Gehrt, Gergits & Fritzell, 2008; Hirsch, Prange, Hauver & Gehrt, 2013; Pitt, Larivière & Messier, 2008; Prange, Gehrt & Hauver, 2011) and establish dominance hierarchies (Barash, 1974; Gehrt & Fritzell, 1999; Hauver, Hirsch, Prange, Dubach & Gehrt, 2013). The raccoon is an omnivorous generalist that exhibits great behavioural flexibility, which has also been linked with complex cognitive abilities (Mikhalevich, Powell & Logan, 2017). The raccoon acts as both forager and hunter, exploiting a vast number of food sources including nuts, fruits, eggs, crustaceans, fish, insects, rodents, carrion and human crops and refuse (Zeveloff, 2002). This requires the raccoon to employ a wide variety of skills in order to survive. Their adaptability has consequently resulted in a population explosion within human cities where they can easily obtain food.

The general lack of knowledge about the raccoon is problematic for this very reason. Diseases like rabies can rapidly sweep through dense urban populations, putting humans and other animals at great risk (Hirsch et al., 2013). The raccoon has also established itself as an invasive species in Europe and Asia, where it has become a threat to local fauna as both a predator and carrier of disease (Beltrán-Beck, García, Gortázar, 2012; Frantz, Cyriacks & Schely, 2005; Ikeda, Asano, Matoba & Abe, 2004). Improved management of this species requires a better comprehension of its cognition, which includes such basic abilities as object permanence. In this study, we aim to remedy this gap in the literature by exploring the development and extent of raccoons' understanding of objects.

Study 1

This study investigated the development of object permanence in infant raccoons (kits). A group of 12-week-old kits and another group of 16-week-old kits were given VD tests. We predicted that raccoons would likely pass SVDs by 12 weeks, having been fully weaned, and certainly by 16 weeks, when a kit can survive independently from its mother. We also expected that kits would be able to pass MVDs when they passed SVDs, like kittens and puppies.

Method

All testing was reviewed and approved by the York University Animal Care Committee (protocol #2017-15W) and complied with the laws and ethical guidelines of Ontario, Canada.

Subjects

All raccoons that participated in this study were the common raccoon (*Procyon lotor lotor*). The kits that participated in Study 1 were wild-born orphans that had been rescued and brought to Another Chance Wildlife Rehabilitation Centre in St. Thomas, Ontario, for rehabilitation and eventual release back to the wild. The first group of eleven kits were approximately 11-12 weeks of age and had been weaned. Several were littermates. Six of these kits were tested. The second group of four kits were not related, and were approximately 16 weeks of age and weaned. All four kits were tested. Both groups had roughly equal numbers of males and females. The kits of each group were housed outdoors together in a large sheltered pen approximately 3 m x 2 m x 3 m in size that was full of toys, climbing equipment, and other enrichment items (see Appendix A). They were taken regularly outside for further enrichment and familiarisation with skills they would need in the wild, such as fishing and tree climbing. At five months of age they were released at a local wild site approved by the Ministry of Natural Resources.

All participants appeared healthy, exhibited species-typical behaviour, and were vaccinated and given a clean bill of health by the local veterinarian. Participation in the tests was voluntary. Subjects were not deprived of food or water during the study, however testing occurred before regular feeding time to ensure motivation. Testing took place in June and July of 2017.

Materials

The original apparatus used was loosely based on that of Barth & Call (2006), but scaled down by approximately one third to be anatomically appropriate for raccoons. A 12” wooden board was used with three small 1.75 oz opaque cups placed on it in a row. This initial apparatus presented several difficulties, as the cups used as occluders appeared to be as rewarding for the kits as the actual rewards. Different rewards were used, including arrowroot cookies, grapes, cherries and toy balls with a bell inside, but to no effect. To prevent olfactory cues, all cups contained the scent of food rewards, however even when non-edible rewards were used and the cups did not smell like food, the cups were still of great interest. The cups had been left with the raccoon kits weeks earlier so that they would habituate to them, but this appeared to make no difference.

An attempt made to modify the apparatus to make it more ecologically relevant, involving a tray filled with rocks and water with heavy ceramic ramekins as hiding places to mimic fishing, was a complete failure. The distracted kits played with the rocks and water, and stole the ramekins. Again, little interest was shown in the rewards. However, presented without any other distractions, the raccoons were still highly motivated to obtain the food rewards and toy balls.

Thus in order to minimize the distraction of the cups, we returned to the original design but screwed the cups down to the board on their sides (see Figure 2). This slightly modified apparatus was placed in the pen until the raccoons were habituated and showed no particular interest in it. When tested again, grapes were used, and the inside of each cup was covered in grape juice to control for odour cues.

Figure 2. The final apparatus used to test the kits in Study 1.

Procedure

The kits were tested in their home pen through the fencing of their home enclosure (see Appendix B). Any attempts to test a raccoon kit alone, either in a smaller pen or with its conspecifics locked in the adjacent feeding area, resulted in emotional distress for the raccoons and no interest in the experimenter or rewards. To compensate, one experimenter (SM) distracted the other raccoons, while the other (JC) secured the attention of one subject.

After having engaged a subject, a reward was hidden beneath one of the three cups; a random number generator determined which cup was baited on each trial. The board was then pushed up against the fence to allow the subject to make a selection. After a selection was made, the subject was allowed to eat the food reward, regardless if the selection was correct. The first cup investigated was considered their selection. Intervals between trials were kept short (~5 s) to compensate for the kits' extremely short attention spans. If a kit became distracted, there was often a much longer intertrial interval (up to several minutes) during which its attention had to be regained. The experimenter wore sunglasses and a hat to prevent any inadvertent cueing, and remained motionless while the kit made a selection.

Data analysis

All analyses were performed in R 3.3.1 (R Core Team, 2018). One-tailed exact binomial tests[8] were used to determine if each participant selected above chance level ($p < .013$) with Bonferroni correction for familywise error.

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[8] Fedor et al. (2008) have argued against the use of t tests in object permanence testing as binomial tests are actually more statistically appropriate. This is presumably because of the extremely small sample sizes, which violate assumptions of normality and have very low power.

Results

Three participants from the group of 12-week-old raccoons were first given 6 three-choice SVD trials. The number of participants and trials was low due to issues engaging the kits' attention. The kits did not select the correct cup significantly above the chance level of 33.3% in the three-choice SVD (Binomial test, *p* = .671). Only one individual made one correct choice.

An easier version of the SVD test with only two choices was then given two days later to the same group. This time six participants engaged with the experimenter for 10 trials each (*n* = 60). The kits did not select the correct cup significantly above the chance level of 50% in the two-choice SVD (Binomial test, *p* = .366). The kit with the highest performance (8/10 correct) was not above chance (Binomial test, *p* = .109).

Four participants from a different group of 16-week-old raccoons were given 29 three-choice SVD trials. Participants did not select the correct cup significantly above the chance level of 33.3% (Binomial test, *p* = .431). The kit with the highest performance (4/7 correct) was not above chance (Binomial test, *p* = .232).

Given that no kit passed any of the simple OP tasks, no further tests were administered.

Discussion

The results from Study 1 indicate that kits of 12 and 16 weeks of age cannot solve SVD tests. This was unexpected, as both cats and dogs have been shown to pass both SVD and MVDs by 7-8 weeks, when they begin to be weaned (Dumas & Doré, 1989; Gagnon & Doré, 1994). However, raccoons are often not fully weaned until 16 weeks (Schneider, Mech & Tester, 1971), although the kits at Another Chance Wildlife Rehabilitation Centre had been fully weaned before testing. In their natural environment, kits begin leaving the den and accompanying their mother from 7-12 weeks (Zeveloff, 2002), and therefore they should be familiar with hunting and foraging by this age despite not being completely weaned. The kits at the rehab centre were not abnormal in this respect, as part of their enrichment included experience climbing trees, foraging for natural foods distributed in their enclosure, and hunting for minnows in pools. However, the possibility that the kits in the rehab clinic were cognitively unusual cannot be discounted since they were raised without their mothers and may have experienced trauma before rescue; however, it is very unlikely that this was the case in light of their good health, normal development, and expression of species' typical behaviours.

It is also possible that raccoons are more like primates than carnivores, and develop OP later in their development. Infant squirrel monkeys do not appear capable of SVDs, even with extensive training, until 36 weeks of age (Vaughter et al., 1972), although other researchers have trained other macaque species to respond correctly on SVDs by 4-8 weeks (Parker, 1977; Wise et al., 1974). Unfortunately we could not test the kits past 16 weeks, as they were released back to the wild shortly after this time. However, since kits in the wild or released from rescue centres forage and hunt independently at this time, one would expect that OP would be fully developed. The other alternative is that OP is learned with extensive experience and/or relies on further physiological development. Kits are often not fully independent from their mother until early the next spring (Gehrt & Fritzell, 1998a), their brains are not fully adult-sized until 20-24 weeks (Michels et al., 1961), and they do not reach full adult size until 2 years of age (Zeveloff, 2002). This indicates a long maturation period, which may function to allow the raccoon to learn the broad range of skills that enables their behavioural flexibility.

Another problem could be the method of testing. Traditional Piagetian testing has been criticized as being inappropriate for monkey species because it requires long interactions with the experimenter (de Blois et al., 1998; Fedor et al., 2008; Mendes & Huber, 2004). Certainly the raccoons had serious issues with attention, which greatly reduced the number of participants and trials that could take place. Raccoons are notorious for their poor attention (Cole, 1907; Davis, 1907; Davis, 1984). Moreover, it is not natural for raccoons to engage for an extended period of time with conspecifics, never mind a human experimenter. Unless engaged in playing, mating or fighting, raccoons do not attend to each other (Cole, 1907; Cole, 1912; Shepherd, 1911). Also, although adult raccoons may have good memory for short-term locations (Hunter, 1913), the kits' short-term memory may still be extremely short. Several other researchers have used expectancy violation testing for OP (Baillargeon, 1987; Hughes & Santos, 2012; Johnson, 2015), which may prove to be a more successful method to use with raccoons.

However, even with the difficulties encountered in testing, it appears that even the youngest kits have reached Stage IV, as we found they would readily check a single hiding place after viewing an object concealed within. However, it would be impossible to disentangle their readiness to retrieve items from hiding places from their compulsion to investigate all crevasses and openings. The raccoon has a very strong instinct to explore its environment with touch; Cole (1912) noted that even when his raccoons were hungry, they would stop working in order to explore a coat pocket. In a discrimination experiment by Cole & Long (1909), in which the raccoons were supposed to select a container based on colour, they found that the raccoons "could not pass by a single food container without both reaching into it and looking into it," and they had to completely redesign their apparatus (p. 665). This is similar to our own experience with the kits, and the reason why our cups had to be screwed down despite having previously habituated the raccoons to them. Stanton et al. (2012) also found that their participants preferred to play with their task items rather than complete the task for the reward. Raccoons tend to be as motivated by exploration and manipulation as they are by food rewards (Breland & Breland, 1961; Cole, 1907; Davis, 1984; Thackray & Michels, 1958).

Study 2

The results of Study 1, indicating that kits as old as 14 weeks could not pass VDs, were unexpected. The purpose of Study 2 was to determine whether adult raccoons were capable of passing VDs. We also gave the adults both traditional and non-traditional IDs. We predicted that adult raccoons would pass both SVDs and MVDs, and could possibly pass transpositions like sloth bears.

Method

Subjects

All testing was reviewed and approved by the York University Animal Care Committee (protocol #2017-15W) and complied with the laws and ethical guidelines of Ontario, Canada.

The adult raccoons tested in Study 2 were wild-born orphans that have been rescued and raised at the BC Wildlife Park in Kamloops, British Columbia. A 6-year-old male ("Chester") and 4-year-old female ("Beatrice") participated in the study. The raccoons were housed together in a naturalistic enclosure approximately 20 m x 20 m x 8 m in size (see Appendix A). The subjects were fully habituated to humans and were trained to be fed individually by their keepers, although other types of interactions with humans were limited.

Both raccoons were vaccinated, healthy, and exhibited species-typical behaviour. None of the raccoons had prior experience in other scientific experiments. Participation in the test trials was voluntary. Subjects were not deprived of food or water during the study, though they were tested before regular feeding time. Testing took place in the spring and summer of 2018 to ensure that the raccoons were not lethargic from wintertime torpor.

Materials

Three 20 oz. cardboard coffee cups were used as occluders for the adult raccoons (see Figure 3). The subjects had no prior experience with the cups, but they did not show more interest in the cups than the food reward. Almonds were used as the food reward, and the interior of all of the cups were smeared with peanut butter to obscure the scent.

Figure 3. The occluders and platform used to test the adult raccoons in Study 2.

Procedure

The raccoons were tested at their individual feeding stations, which were flat tree stumps secured into the enclosure substrate (see Appendix B). The three cups were placed on their sides spaced 20 cm apart at a distance of .5 m. Pilot testing was conducted to ensure they could not see into the cups from that distance.

The subject's attention was caught by waving the almond reward in front of them. The experimenter (SM) ensured that they were visually tracking the reward before placing it in a cup. After a 1-2 s delay, the raccoon made a choice. The first cup investigated was considered their selection. If the cup contained an almond, the participant was able to retrieve it. If the cup did not contain an almond, the raccoon was not rewarded. The next trial was then set up; the average inter-trial interval was ~10 s. A random number generator determined which cup was baited on each trial. Again, the experimenter wore sunglasses and a hat to avoid cueing, and stayed motionless while the raccoon made a selection.

For the invisible displacement version of the task, the experimenter hid the almond in her hand then placed her hand in the cup, left the almond inside, then showed her empty hand to the subject. The subject was then allowed to make a selection.

Tests

Single Visible Displacement (SVD): The experimenter places the reward under one cup.

Multiple Visible Displacement (MVD): The experimenter places the reward under one cup, then visibly removes it and places it into another cup.

Multiple Visible Displacement Control (MVD control): The experimenter places the reward under one cup, then visibly removes it and places it into another cup, then lifts the remaining empty cup.

Single Invisible Displacement (SID): The experimenter places the reward in their hand, places their hand under a cup and invisibly removes the reward, then shows the hand empty.

Transposition: The experimenter places the reward under one cup, then swaps the rewarded cup's position with an empty cup.

Rotation: The experimenter places the reward under one cup, then rotates the platform 180˚. Only the external cups were used as hiding locations.

Data analysis

All analyses were performed in R 3.3.1 (R Core Team, 2018). One-tailed exact binomial tests were used to determine if each participant selected above chance level in Study 2 ($p < .007$) with Bonferroni correction for familywise error.

Results

Two adult raccoons participated in 20 three-choice SVD trials. Both participants selected the correct cup significantly above the chance level of 33.3% in the three-choice SVD (Binomial test, $p < .001$). Individual analyses revealed that the male raccoon, Chester, performed above chance (Binomial test, $p < .001$) as did the female raccoon, Beatrice (Binomial test, $p < .001$). Both raccoons failed to respond to the SID test.

The adults were given additional tests 10 weeks later. Chester did not participate this time, but Beatrice participated in 6 trials each for MVD, MVD control, transposition and rotation. Beatrice failed to select the correct cup significantly above the chance level of 33.3% in the MVD (Binomial test, $p < .407$) or control MVD (Binomial test, $p = .407$) tests. Error analysis revealed that Beatrice selected the first cup visited by the experimenter above chance in both conditions (Binomial test, $p = .001$). Beatrice did not select a single correct cup in either the transposition or rotation conditions, however error analysis revealed that Beatrice selected the initially rewarded location above chance in both conditions (Binomial test, $p < .001$).

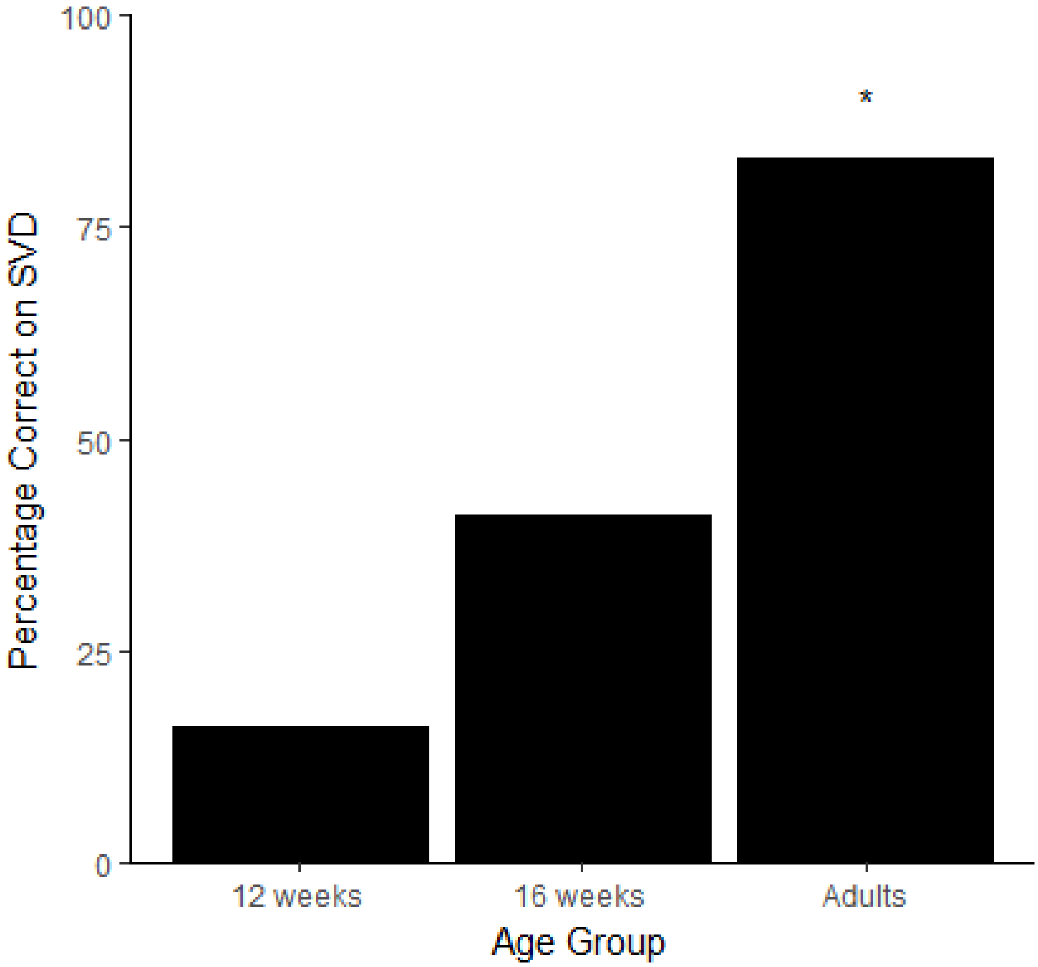

Figure 4. Percentage correct by each group on three-choice SVDs. The 12 week group and 16 week group data is from Study 1, the adult group data is from Study 2. *$p < .007$

Discussion

By adulthood, it is evident that raccoons can solve SVDs. Our female participant, Beatrice, performed extraordinarily well, making no errors on the early trials, including no A-not-B errors. Out of 20 trials, she only made two mistakes. On the other hand, Chester, our male participant, seemed to have an initial difficulty understanding the task and made errors on the first three trials. He appeared to have a side bias toward selecting cup C, which is a common finding throughout OP research (see for example Anderson, 2012; Auersperg et al., 2014; de Blois & Novak, 1994; Dumas & Brunet, 1994; Jaakkola et al., 2010; Müller, Riemer, Range & Huber, 2014; Nawroth et al., 2015; Schino et al., 1990). However, after these initial errors, Chester only made two other errors later in the task, and his overall performance was above chance. It seems extremely unlikely that the raccoons were using the strategy of selecting the only cup manipulated by the experimenter because otherwise they should not have failed to respond in the SIDs.

For the same reason, it is also unlikely that the raccoons were using olfaction to solve the task. We were careful to mask the reward scent by smearing peanut butter in all of the cups, a method that has worked successfully for other researchers working with primates and carnivores (Deppe et al., 2009; Fiset & Plourde, 2013; Hartmann et al., 2017). Tests for the use of olfaction in dogs, cats and bears, including covertly hiding the food reward in the wrong cup (Triana & Pasnak, 1981), hiding the food reward with no visual cues (Amici et al., 2017), and extensive odour masking (Gagnon & Doré, 1992), have indicated that these carnivores do not use olfaction to successfully solve displacements. In raccoon testing, Cole & Long (1909) controlled for odours in their colour discrimination task by hiding food rewards in all of the containers in half of their trials, and they found no effect on the raccoons' performance. In a further odour test, they found that the raccoons could only find an odour by sniffing very closely to its location (Cole & Long, 1909). Cole had observed on other occasions that raccoons did not appear to rely on their sense of smell, such as failing to find meat hidden in the hay until it was within a few inches of their nose (Cole, 1907; Cole 1912). However, a recent study by Kent & Tang-Martínez (2014) has revealed that raccoons can distinguish between different individuals' urine, so it would be a mistake to assume that raccoons are completely deficient in their olfactory abilities. Still, the general consensus appears to be that raccoons are an overwhelmingly tactile species.

Beatrice's failure on the MVD is unusual. Typically, carnivores that can pass SVDs also pass MVDs; it has been hypothesized that some carnivores develop allocentric abilities early because they are mobile from birth (Dumas & Doré, 1989). Raccoons, on the other hand, are not mobile until 4-6 weeks (Zeveloff, 2002). However, they should have plenty of time by adulthood to learn to track an object hidden at multiple locations. Beatrice selected the first cup and second cup visited by the reward equally; on MVD control trials, she never selected the empty cup lifted by the experimenter. Thus, she appears to have ignored the experimenter's actions, but both locations of the reward seem to have been equally activated in her working memory. This makes raccoons unlike cats, which deactivate from working memory a location that a reward has visibly left (Goulet et al., 1994; Goulet et al., 1996). Raccoons do differ from cats in that they do not solely rely on hunting to survive, but it is still unexpected that their tracking would be so poor. As this test was conducted only with one subject, it seems premature to rule out that raccoons are incapable of MVDs.

The lack of success by Beatrice on the transposition and rotation tests was less unexpected, especially as she and Chester did not pass the SID test. Dogs, wolves and cats cannot pass transpositions or rotations (Doré et al., 1996; Fiset & Plourde, 2013; Miller, Gipson, Vaughan, Rayburn-Reeves, & Zentall, 2009; Rooijakkers et al., 2009), and they are challenging for great apes and children (Barth & Call, 2006; Lasky et al., 1980; Sophian 1986). Still, new evidence indicates that sloth bears can succeed on transpositions, even with controls for practical strategies and other sensory cues (Hartmann et al., 2017). Like the raccoon, the bear is an omnivorous forager and hunter, which Hartmann et al. (2017) believes has contributed to the sloth bear's OP abilities. However, Beatrice the raccoon did not succeed on a single trial of either test. Error analysis revealed that she did significantly select the initial location of the reward, a behaviour commonly seen by other nonhuman animals that do not track invisible objects. For example, cats always look wherever the food was last seen, even in an obviously empty displacer (Doré, 1990). Again, although it seems likely that raccoons cannot pass these tests, with only one subject tested it is too early to make a definitive statement.

Triana & Pasnak (1981) have argued that power studies are useful for OP tests because a few successful individuals can demonstrate which abilities are within a species' capacity; on the other hand, failures by a few does not mean a behaviour is beyond a species, either. Due to practical constraints, this experiment was limited in its number of participants. Much more testing needs to be conducted before conclusions can be reached about the limits of the abilities of raccoons, particularly because raccoons are notorious for their substantial individual differences. Many studies have made note of one raccoon that vastly outstrips the others in its performance (Hunter, 1913; McDougall & McDougall, 1931; Shell & Riopelle, 1957; Shepherd, 1911a; Thackray & Michels, 1958), or in one case, performs far worse (Johnson, 1961). Only two of the eight raccoons in Stanton et al.'s (2012) experiment could successfully learn the Aesop's fable task, and their participants exhibited a wide variation in learning patterns: one raccoon showed an increase in time over trials, another a decrease in time, and yet another was consistent. Stanton et al. (2012) and Shell & Riopelle (1957) have both found significant individual differences in their experiments.

There are other considerations that need to be taken into account as well. It has been suggested that male and female raccoons may significantly vary in their cognitive abilities, as females were found to be significantly less likely captured by traps, but not for any clear ecological reasons (Gehrt & Fritzell, 1996b). This possible sex difference has never been formally tested. Females and males do differ greatly in their life histories. Females take on the complete burden of raising offspring, and generally live independently in small territories near resources (Gehrt & Fritzell, 1998b; Gehrt & Fritzell, 1999). Females will share territory with close relatives and may even share dens, especially in colder climates (Gehrt & Fritzell, 1998a; Robert, Garant, Vander Wal & Pelletier, 2013), but they are typically asocial compared to males (Pitt et al., 2008; Prange et al., 2011). Unrelated males, on the other hand, form and associate in groups of three to four which encompass large territories, although some males do remain solitary (Gehrt & Fritzell, 1997; Gehrt & Fritzell, 1998b; Gehrt et al., 2008; Hirsch et al., 2013; Pitt et al., 2008; Prange et al., 2011). Unlike females, yearling males leave their natal territory (Fritzell, 1978; Gehrt & Fritzell, 1998a), and therefore must contend with an unfamiliar environment and a pre-existing male dominance hierarchy (Barash, 1974; Pitt et al., 2008). Males and females only associate during breeding season and rest together for extended periods in what Gehrt & Fritzell (1996a, 1999) have referred to as “consortship.” These consortships do not appear to successfully function to monopolize access to a female during estrus, as paternity tests conducted on raccoons in Southern Illinois revealed that most litters were sired by multiple males (Roy Nielsen & Nielsen, 2007). It is also possible that performance varies in adults by age; Davis (1907) observed that his older adults (3-4 years) behaved quite differently to the younger adults (1.5-2 years), working with more efficiency but less energy. Thus experience may continue to modify raccoon behaviour, even into adulthood.

Raccoon behaviour is also affected by seasonal changes. We were careful to test the raccoons after winter had passed, as several researchers have noted that raccoons are slow or refused to work during torpor (Hunter, 1913; Hunter, 1928; Munn, 1930). Davis (1984) also found that his male raccoon subject became difficult to manage during mating season. Consequently, participants' behaviour and motivation may vary according to time of year, and these factors need to be taken into account in addition to potential sex differences, age differences, variations in individual ability and individual temperament. As is clear from our own experience and other researchers' accounts, raccoons are very challenging to test and their results difficult to interpret. However, it is worth continuing to study these charismatic carnivores that with whom we share our cities in order to better our understanding and management.

General Conclusion

As is not uncommon in science, these studies pose more questions than they answer, in no small part because so few experiments have been conducted in the area of raccoon cognition. Our research has served as a preliminary glance at the raccoon's potential OP abilities. Our results indicate that raccoons develop the ability to represent SVDs late into their maturation, after they have been weaned and can survive independently. Thus experience and/or further physiological development appear to be non-negligible factors in SVD abilities. Our adult female subject did not succeed on MVDs, SIDs, transpositions or rotations, and so whether any raccoons can succeed beyond basic SVDs (Piaget's Stage Va) is unknown. More research will need to be conducted with more participants, as historically raccoons are known for extreme individual differences. It is also possible that traditional Piagetian tests are unsuitable for raccoons due to the necessity for prolonged social interaction and their short attention span. Alternative testing methods should be considered. However, based on our subject’s behaviour in transpositions and rotations, it appears unlikely that raccoons can track unseen objects. Therefore, our results support that, like other carnivores, raccoons cannot represent invisible objects, and are thus consequently limited to Stage V object permanence.

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Appendix A

Raccoon Enclosures

The enclosure used to house the kits of Study 1 at Another Chance Wildlife Rehabilitation Centre.

The enclosure used to house the adult raccoons of Study 2 at BC Wildlife Park.

Appendix B

Raccoon Testing Areas

The kits’ testing location at the enclosure fence for Study 1.

The feeding station where the adult raccoons were tested for Study 2.