Chapter 7
Cognitive Development in Gray Wolves: Development of Object Permanence and Sensorimotor Intelligence with Respect to Domestic Dogs

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Abstract In this chapter, we explore whether domestic dogs and gray wolves share a similar cognitive development with regards to how they represent physical and/or social objects. To reach this objective, we examine two key components of the Piagetian theory of cognitive development in the gray wolf: object permanence and sensorimotor intelligence. We detail how the capacity to search and locate disappearing objects develops in wolves and compare these data with those observed in previous studies with dogs. We then further describe an observational study of sensorimotor intelligence with these wolves. Overall, the results suggest that the development of object permanence is similar in dogs and wolves, both species reaching Stage 5b of object permanence by the age of 11 weeks. In terms of sensorimotor intelligence, Stage 4 was the upper limit of sensorimotor intelligence we observed in wolves. Moreover, up to 6 weeks of age, the behaviors of wolf puppies are directed predominantly towards their conspecifics, and by Week 8, wolves' interest in inanimate object increases significantly. In discussion, we explore the factors affecting the development of object permanence and sensorimotor intelligence in canines.

7.1 Introduction

In the last two decades, the scientific study of cognition in the domestic dog has grown substantially. For example, the Web of Sciences index (Thompson Reuters) reveals that the rate of publications about cognition of domestic dogs (using dogs,

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behavior and cognition as keywords) has increased at a mean rate of 35 % per year since the year 1991. Without entering into the reasons that can be put forward to explain this strong interest in the study of the domestic dog's mental capacities [as a starting point, readers are invited to consult Bradshaw (2011) and Miklósi (2007)], it is worth mentioning that the domestic dog's cognition is now investigated from different points of view by several disciplines: behavioral biology, behavioral ecology, comparative psychology, ethology, evolutionary anthropology, functional morphology, and veterinary behavior, to name a few. From a psychological perspective, the Piagetian theory of cognitive development, which was initially developed by Piaget (1954) during the course of his observations of his own children, is one of the most fruitful theoretical frameworks used to study animals' cognition (Pepperberg 2002), including dogs' (e.g. see Fiset and Plourde 2013).

Piaget (1954) divided the general development of children's intelligence into four general periods, from birth to adolescence. The first period of cognitive development, namely the sensorimotor period, is of most interest for comparative researchers since it primarily focuses on the organism's sensory perception and motor activities. Moreover, since the Piagetian's tasks used to measure the cognitive development during the sensorimotor period are easily adaptable to the natural behaviors of non-verbal animals, by the end of the 1970s, the Piagetian theory was endorsed by researchers to investigate the development of cognition in animals (for a summary, see Doré and Dumas 1987). More specifically, the sensorimotor period is characterized by the development of various concepts, such as object permanence (OP), space, time, causality and a general capacity, called sensorimotor intelligence (SI). In the present study, in the context of canine's cognition, we concentrated our attention on two key concepts of the sensorimotor period, that is, OP and SI.

OP is defined as the knowledge that social or physical objects still continue to exist when they are no longer present in one's visual field. In canines, like dogs and wolves, OP is essential for survival. For instance, the capacity to mentally represent a disappearing object is useful in predatory situations, where a prey has moved behind an obstacle (e.g. a tree), or in a social context, when different members of a group move around and momentarily disappear from sight. SI, for its part, is characterized by the organization and coordination of different schemas of action in several logical steps. In the Piagetian sensorimotor period, the repetition of a particular behavior in different circumstances results in a common attribute called a schema of action. It is also the organism's cognitive structure that organizes and coordinates its behavior in logical sequences (Doré and Dumas 1987). As experiences happen in one's life, these schemas of action are modulated, allowing the organism to generalize and transpose its behaviors and/or mental processes to new and different situations. In the Piagetian framework, OP and SI are closely interconnected during the sensorimotor period and both cognitive capacities develop at the same rate through a series of six distinct stages.

During the first two stages of OP, children lack interest in disappearing objects. Thus, they do not exhibit actions when objects disappear from their visual field.

They are, however, capable of briefly following them with their head or body. During the third stage, visuomotor coordination is established and children gain the ability to retrieve partially hidden objects. In Stage 4a, they become capable of retrieving hidden objects, but solely if they initiated a search movement toward the hiding location before the final disappearance of the object. Such a movement ceases to be necessary in the subsequent substage (Stage 4b), and children can now find an object they saw disappear at a specific location. It is also in this stage that the A-not-B error emerges. It manifests when children successively search in the last location they saw the object prior to its disappearance.

Stage 5a of OP marks when children stop committing the A-not-B error, and become capable of retrieving visibly hidden objects in several different locations. In Stage 5b, children can retrieve an object they saw disappear successively in several hiding locations. In the sixth and last stage, children gain understanding of invisible displacements. In Stage 6a, they are capable of solving simple invisible displacement problems. In these problems, an object is first hidden inside a transportation device (i.e. a cup or a hand) and this device is moved behind a box or a screen. There, the object is imperceptibly transferred from the transport container to the hiding location. Since the child cannot perceive either the displacement of the object from one location to another or the transfer of the object from the transportation device to the target location, the displacement is considered invisible. The child must mentally infer the displacement to localize the position of the object. In Stage 6b, children master the ability to relocate objects that were successively hidden in different locations using invisible displacements.

The ontogenetic development of OP in canines has, so far, only been investigated by Gagnon and Doré (1994), who conducted a study on the domestic dog. These authors used a cross-sectional study to assess the stages of OP reached by dogs as a function of age. Most specifically, they selected seven groups of dogs: five of which were young puppies of 4–8 weeks old, and the last two groups included dogs of 3 and 9 months-old. In their study, Gagnon and Doré adapted a procedure previously developed by Dumas and Doré (1987, 1989) for domestic cats for dogs. In their study, the dogs' task was to track and find an attractive object (a toy) that moved and disappeared behind a series of opaque screens. When a group failed a particular task, the same task was administered to the next oldest group and so on. Overall, Gagnon and Doré (1994) found that dogs' understanding of OP developed gradually from 4 to 8 weeks of age. Most specifically, their results revealed that the different stages of OP in dogs emerge as follows: Stage 2 (4 weeks), Stage 3 (5 weeks), Stage 4a (6 weeks), Stage 5a (7 weeks) and Stage 5b (8 weeks). As a group, the dogs did not reach the understanding of invisible displacement, but 11-month-old dogs succeeded at problems of Stage 6a, suggesting an understanding of invisible displacement in older dogs, supporting previous works by Gagnon and Doré (1992) in adult dogs (for an alternative interpretation, however, see Collier-Baker et al. 2004; Fiset and LeBlanc 2007).

SI also develops throughout a series of six stages in which schemas are acquired and modified through direct exploration of the world and its objects. In Stage 1, the behaviors are limited to the reflexes (e.g. suckling) of organisms.

The appearance of a child's first habits, known as primary circular reactions, characterizes the second stage. These behaviors revolve around oneself (e.g. putting his thumb in his mouth) and are repeated over and over, as they produce reactions that the child finds interesting. Next, in Stage 3, secondary circular reactions make their appearance. Secondary circular reactions, contrary to primary circular reactions, are repeated actions towards external objects (either physical or social) rather than oneself. Secondary circular reactions are intentionally repeated and are not coincidental. For instance, an infant extends his hand to grab an object close to him in order to play with it.

Stage 4 of SI corresponds to the coordination of two schemas of action, and consolidates the role of intention in children as illustrated by the emergence of imitation. Schemas are no longer repeated to produce long-lasting fortuitous stimulations, but to obtain an intentional result. For instance, a child throws away a first toy in order to grab a second toy, which is later put in his mouth. Stage 4 is succeeded by Stage 5, in which tertiary circular reactions make their appearance. These reactions introduce the notion of behavioral variation in the intentional repetitions of actions on external objects (either physical or social). An example of this period of trial-and-error is when a child produces different sounds (using cries or hitting toys together) to attract the attention of his caregiver. Finally, Stage 6 (early mental representation) corresponds to the invention of new combinations of actions. In Stage 6, children search for ways to pursue a goal, but, contrary to the preceding stages, this process is done mentally, without the need to experiment on the external object beforehand. For instance, a child exposed to different toys selects the one that is the most likely to make the loudest noise when shaken.

To our knowledge, only Frank and Frank (1985) used the Piagetian's framework of SI to interpret the cognitive development of canines. Most specifically, these authors administered a series of puzzle boxes of increasing complexity to 10-week-old dogs (Malamute) and wolf pups, and the animals' task was to perform increasingly complex manipulations to extract a food dish from a box. Frank and Frank's results suggest that wolves demonstrate behaviors of Stage 5, possibly 6, of SI, while dogs only demonstrate responses of Stage 3, maybe 4. However, as rightly pointed out by Frank and Frank (1985), their conclusions about the acquisition of Stage 5 and/or 6 are doubtful since the wolves were probably able to use skills from inferior stages of SI (e.g. Stage 3 and/or 4) to solve the most complex tasks used in their study.

In order to depict the ontogenetic development of cognition in canines, the first objective of the current study was to determine the development of OP in the gray wolf and compare it with the results observed by Gagnon and Doré (1994) in the domestic dog. To reach this objective, similarly to Gagnon and Doré (1994), we used the scale developed by Uzgiris and Hunt (1975) in human children. Actually, our experimental procedures, as well as the dimensions of our material in the tests of OP, were exactly the same as the ones used by Gagnon and Doré (1994). However, given the small number of wolves that we were able to work with, in contrast to Gagnon and Doré (1994) who used a cross-sectional approach, we used a longitudinal approach in which the same animal is tested several times during the course of its development. It is worth noting that longitudinal studies are frequently used by researchers who deal with reduced sample size when investigating the development of OP (for an example in various animal species, see Pollok et al. 2000; Ujfalussy et al. 2012; Zucca et al. 2007).

The present study also aimed to corroborate the conclusions of Frank and Frank (1985) by establishing an overview of the development of SI in the gray wolf. To do so, we adapted the procedures used by Dumas and Doré (1991) in domestic cats and recorded the natural behaviors of the wolves between their fourth and 11th weeks of life. Finally, since Dumas and Doré (1991) observed that domestic cats attain Stage 5b of OP but solely Stage 4 of SI, we wanted to determine whether or not, in canines, the development of SI synchronized with the development of OP.

7.2 Wolf Study

7.2.1 Method

Participants Four gray wolves (three females and one male) from the same litter began this study. The wolves were from Wolf Park, Battle Ground, Indiana (USA), and had been hand-reared for human socialization from the age of 10 days, as described by Klinghammer and Goodmann (1987). Human caretakers were in contact with the pups 24 h a day, from day 10 to day 28. After 4 weeks, the caretakers reduced the contact with the pups to 16 h a day. Intense human socialization was stopped when the wolves were four months old. Afterward, the wolves were still in regular contact with humans for health care, feeding and behavioral studies.

The wolves were all sick between Day 38 and Day 51, and the study was postponed during this critical period of development. Moreover, one wolf, Devra unexpectedly died on Day 56 of an unknown illness. To determine the cause of death (the autopsy later revealed a congenital liver shunt) and make sure it was not contagious, we interrupted the study a second time from Day 56 to Day 61 before resuming with the three remaining wolves. Given that Devra was tested inconsistently in the OP tests before her death, all her data in the tests were removed from the study. Consequently, our conclusions about the development of OP were limited to the three wolves that completed the study. However, Devra's data in the observational phase of the study were kept until her death, and were adjusted accordingly.

Apparatus In the observational phase of SI (see procedure), the wolves' behaviors were recorded via a Sony HDR-CX110 digital video camera fixed on a tripod. To stimulate the behavior of the wolves, several objects of diverse sizes and forms (puppets, towels, cardboard boxes, ropes, etc.) were disposed on the floor of the room or on the ground inside the outdoor enclosure.

In the OP tests (see procedure), three identical painted white wooden boxes (17 cm wide × 19.5 cm high × 11.5 cm deep with a top, a bottom, a front, and two side panels) served to hide the target object. The bottom of each box was filled with lead bars to increase inertia. They were arrayed in a semicircle at a distance of 30 cm from each other and were equidistant (150 cm) from the wolf's position. In order to maintain the wolves' motivation to search for the target object, different objects were used. The objects were either an orange rubber ball (handled by a translucent nylon thread that was tied to it), a cardboard tube, a small puppet or a white towel. In the invisible displacement trials (see procedure), a small wooden box (9 cm wide × 15 cm high × 9 cm deep), without the top and front panels, was also used. The inside of this box (called *displacement device*) was painted black and its outside was painted white. To help its manipulation, a 117 cm vertical plastic stick was fixed on the back of this box. To reduce the possibility that the wolves used olfaction to find the target object, rose water (1/10 diluted in water) was sprayed over the apparatus. This solution is well known for masking olfaction in canines (Gagnon and Doré 1992). Each trial was recorded via a Zi6 Kodak HD digital video camera fixed on a tripod placed behind the animal.

Procedure At the beginning of the study, the wolves were three weeks of age. Two different approaches were used to assess the development of SI and OP. SI was assessed via the recording of wolves' spontaneous behavior and OP was tested via a series of formal tests administered to each wolf.

7.2.2 Behavioral Observation of Sensorimotor Intelligence

The wolves' spontaneous behavior was recorded from Week 4 to Week 11. As did Dumas and Doré (1991), who studied SI in domestic cats, we recorded the wolves' behavior in intervals of 10 min. However, although we had initially planned to record the wolves' individual behavior three times a week, we were not able to follow the schedule as planned. This divergence from the planned recording schedule was mostly due to (i) the great amount of time needed by the human caregivers to nurture the puppies (feeding, etc.), (ii) the sickness of the animals and (iii) the small amount of time the pups were awake and interacted with each other and/or the toys. The recording schedule was therefore modified. For Weeks 4 and 5, since the wolves' behaviors were limited to the nurturing chamber, we recorded the wolves' behavior as a group. From Weeks 6 to 11, when the wolves were moved to the outdoor enclosure, we were able to record their behaviors individually. However, due to various factors (illness, overbooked testing schedule, etc.), it was impossible to record the behavior of each wolf during each week (see Table 7.1).

The analysis of wolves' spontaneous behavior was based on the behavioral categories identified by Dumas and Doré (1991), who coded domestic cats' SI for each stage of cognitive development during the sensorimotor period. We adapted the criteria used by Dumas and Doré (1991) to the natural behaviors of gray

Table 7.1 Duration (in minutes) of the video recordings as a function of weeks and wolves

Week	Type of recording	Dharma	Devra	Tilly	Gordon
4	Group	———————————————	——50——	———————————————	
5	Group	———————————————	——30——	———————————————	
6	Individual	–	–	10	–
7	Individual	–	–	–	–
8	Individual	10	10	–	–
9	Individual	–	–	–	–
10	Individual	10	–	–	10
11	Individual	–	–	20	10

Note When the duration of recording is marked as higher than 10 min, several 10 min bouts of recording were recorded during this particular week (e.g. 30 = 3 bouts of 10 min)

wolves (see Table 7.2). To be consistent with our approach, circular activities in wolves, a key component of the development of SI, were also coded as described by Dumas and Doré (1991). In short, to be coded as circular (either primary, secondary or tertiary), a behavior had to be repeated a minimum of five times and last 10 s or more during the same action sequence. Given the limited number of bouts we were able to record, the use of these criteria ensured that the behaviors judged as circular were highly repetitive and reflected the natural behavior of wolves. The different behaviors that served to code the development of SI in wolves were as follows: scratching, pawing or kicking, tugging, howling, biting other wolves, wrestling, and gnawing.

7.2.3 Tests of Object Permanence

From Weeks 4–9, the testing took place in the nurturing room. By doing so, we assured that the wolves were familiar with the testing environment (a pilot study performed by Gagnon and Doré (1994) revealed that dog pups' behaviors were perturbed when tested in a new environment). In Weeks 10 and up, the wolves were tested in a quiet and isolated area of the outdoor enclosure.

The acquisition of Stages 2 and 3 of OP was assessed via the administration of a visual pursuit test in the nurturing room. These tests served to evaluate the wolves' perceptual development, most specifically their visuomotor coordination (Dumas and Doré 1989; Gagnon and Doré 1994). In this test, the wolf was not restrained and was free to move of its own will. The experimenter who performed the manipulation (E1) suspended an attractive object (an orange ball) right in front of the wolf. Then, while ensuring that the wolf was looking at the object, E1 slightly moved the object to the right or left of the wolf a few times and then through an arc of 180° (i.e. behind the wolf). If the wolf followed the object up to the point of disappearance in its visual field but failed to look for the object behind itself, Stage

Table 7.2 Criteria used to assess the development of wolves' SI for each stage

Stage 1	*Reflexes* Behavioral expression in pups is due to reflexes that are present at birth (e.g. suckling)
Stage 2	*Primary circular reactions* Reflexes transform to become a pup's primary habits, and manifest under the form of primary circular reactions. These reactions concern the pup's own body, and are triggered by spiking the interest of the pup, who finds it interesting, and then repeats the motion (e.g. scratching, walking)
Stage 3	*Secondary circular reactions* Secondary circular actions are actions that are repeated by the pup and result in an interesting effect with an external object, which may be either physical or social (e.g. tugging a log)
Stage 4	*Coordination of secondary circular reactions* The pup is now able to coordinate two different schemas of action in order to reach a predetermined goal. The pup's actions (e.g. biting, tugging) are directed towards different aspects of the environment (e.g. toys, conspecifics, etc.)
Stage 5	*Tertiary circular reactions* Behavioral variations are now possible. The pup experiments using trial and error, repeating actions that produce interesting effects on social or physical objects (e.g. pulling a branch to get a piece of food or a toy) with constant variations (e.g. with his mouth or his foreleg)
Stage 6	*Early representational thought* The pup is now capable of coordinating mental schemas without the use of direct experimentation on the environment (e.g. putting down a log and taking instead a branch to pull a piece of food toward him)

2 of OP was reached. However, if the wolf was able to follow the object during the entire trajectory and look for the object behind itself, Stage 3 of OP was reached.

Stage 3 and beyond were assessed via a series of formal OP tests. In the OP tests, E1 stood about 50 cm behind the central box and a second experimenter (E2), who restrained the animal by its shoulders, bent on her knees to its left side. At the beginning of each trial, E1 attracted the attention of the wolf by slightly moving the object back and forth about 50 cm in front of the central box. Once the wolf looked at the object, E1 moved the object as described in the tests (see Table 7.3). If the wolf did not pay attention to the manipulation of the object, the trial was rerun. To prevent involuntary cueing, once the object was put down, E1 looked up at E2. Then, E2 released the animal. If the wolf retrieved the object after its first choice, it was reinforced with social rewards (e.g. *Good boy*) and the opportunity to play with the object. However, if the wolf selected a non target box, the object was immediately removed from behind the box and no reward was given.

Six visible displacement tests (1–6) and one invisible displacement test (7) were administered to the wolves. Since our goal was to determine the development of OP, the tests were administered sequentially, from Test 1 to Test 7—that is, all the visible displacement tests were administered first and followed by the invisible displacement test. Each test was composed of 5 trials. To be successful in a test, the wolf had to succeed 4 trials out of 5 (Binomial test, $p = 0.33$, $\alpha = 0.05$). When a wolf succeeded a test, the next test in the sequence was administered as rapidly as possible, usually at a later time in the same day (47 % of the time the next test was administered within the same day). Otherwise, it was administered in the same

Table 7.3 Tests used to assess the development of wolves' OP for each stage

Test	Stage	Description
Test 1	Stage 3	Partial occlusion. E1 partially hid the object behind the target box. The object was always hidden behind the same box (A or C, depending on the wolf)
Test 2	Stage 4a	Single visible displacement–initiation of movement by the animal. E2 released the wolf right before E1 hid the object behind the target box. The object was always hidden behind the same box (A or C) and for each wolf, the target box was the same as the one used in Test 1
Test 3	Stage 4b	Single visible displacement. E2 released the wolf when the object was totally hidden behind the target box. The object was always hidden behind the same box (A or C) and for each wolf, the target box was the same as the one used in Tests 1 and 2
Test 4	Stage 5a	Sequential visible displacement. The object was hidden behind the box located at the opposing end of the row of boxes to the one previously used in Tests 1–3. For example, if the target box in Tests 1–3 was A, in Test 4 it was box C. The object was always hidden behind the same box (A or C). In the first trials of Test 4, if the animal searched at the box used in Tests 1–3, it displayed an A-not-B error
Test 5	Stage 5b	Double visible displacement. E1 first hid the object behind a box. Then, E1 visibly removed the object from the box and moved it behind a second box. Each box (A, B and C) served as first and second box at least once
Test 6	Stage 5b	Triple visible displacement. E1 first hid the object behind a box. Then, E1 visibly removed the object and hid it behind a second box. Next, E1 removed the object from the second box and hid it inside the box not yet visited. If the object was being moved from box A to box C (or from C to A), it always passed in front of box B (never behind). In each trial, every box was visited at least once
Test 7	Stage 6a	Single invisible displacement. At the beginning of a trial, the transportation device was placed at either the right or left end of the row of boxes, its open side facing the wolf. Then, E1 visibly placed the object inside the transportation device and, to hide the object from the wolf's vision, rotated the device on an axis of 180°. Next, E1 moved the device behind one of the three boxes and unnoticeably transferred the object from the device to the target box. After, E1 removed the device from the box and immediately rotated the transportation device to show to the wolf that it was now empty. Finally, E1 brought the device to the other end of the row of boxes from its initial starting location and rotated it on an axis of 180° to hide the fact that it was now empty. The object was always hidden behind the same box (A or C), which was the opposite of the one used in Tests 1–3. For instance, if the target box was A in the three first tests, the object was now hidden in box C

week. The only exception to this rule was Test 4. Since Test 4 served to determine whether or not the wolves commit the A-not-B error, Test 4 was administered immediately after the wolf had succeeded Test 3. If a wolf failed a test (any of them), the same test was rerun later in the same week. However, due to wolves' illness and the death of Devra, it was impossible to follow the schedule as planned. By consequence, on a few occasions, the delay between one test (success or failure) and the next was over 1-week (see Table 7.4).

Table 7.4 Number of correct choices in each test of OP (out of 5) as a function of week, wolf and stage

Week	Wolf	Stage 3	Stage 4		Stage 5			Stage 6
			a	b	a	b	b	a
		Test 1	Test 2	Test 3	Test 4	Test 5	Test 6	Test 7
Week 6	Dharma	4	0					
	Gordon	0, 4	1					
	Tilly	4	0					
Week 8	Dharma		4	4	2			
	Gordon		5	–	–			
	Tilly		5	1	–			
Week 9	Dharma			–	2	–		
	Gordon			5	4	1		
	Tilly			5	5	–		
Week 10	Dharma				3	–	–	–
	Gordon				–	–	–	–
	Tilly				–	4	5	2
Week 11	Dharma				5	5	–	–
	Gordon				–	5	1, 5	1
	Tilly				–	–	–	1
Week 12	Dharma						5	4[a]
	Gordon						–	1
	Tilly						–	–

Note 1 The wolves were ill during Week 7, and so tests were not conducted
Note 2 When two numbers are within the same cell, the wolf was tested two times on the same test within the same week. The first number represents failure and the second represents success
[a] Dharma's score on Test 7 was considered a failure (see text)

7.2.4 Video Analysis

Two coders reviewed the videotapes of the development of SI and of the OP tests. One coder (the second author) viewed all the videos, adapted the coding system, and applied it to the behavior of wolves. For validation purpose, the second coder (the first author) also coded the wolves' behavior by viewing a random selection (50 %) of the SI and OP recordings. Both coders agreed on all behaviors.

7.2.5 Results

7.2.5.1 Development of Sensorimotor Intelligence

Due to the inconsistency of our video recordings (see *Procedure*), instead of quantifying how often the schemas of action associated with each stage occurred, we focused our attention on the presence or absence of these schemas of action.

When a behavior from a specific stage was observed for the first time (regardless of the wolf), we considered this specific day as an indication of the earliest occurrence of any behavior associated with this stage of development. As a consequence, this particular stage of development was then coded as reached by the wolves. Moreover, to specify the nature of the objects the wolves interacted with during each stage of development, we examined the frequency of appearance of behaviors with social and physical objects. To do so, given that the number of video recordings per week varied, we adjusted the frequencies of each behavior as a function of the number of 10 min bouts that were recorded in a week for each wolf. This allowed us to standardize the frequency of each behavior per week.

As mentioned earlier, the pups were already 3-weeks old at the start of the study and were fed by human caretakers. By consequence, behaviors that characterized Stage 1 of the sensorimotor period, which are mostly basic reflexes (e.g. suckling, rooting, Galant's reflex), could not be observed. However, on Day 23, when the observation of the SI of wolves formally began, we noticed that crawling was still occasionally among the behaviors of the wolves. We therefore concluded that the wolves acquired Stage 1 before Day 23 but we could not discern the exact age around which this stage was reached.

Similarly, on Day 23, we also observed primary circular reactions, which are behaviors of Stage 2. For instance, walking on four legs is an example of a primary circular reaction in wolves. This locomotor action has a primarily focus on one's body, and was repeated over and over by the animals. On Day 23, all the wolves were experiencing locomotion on four legs, sometimes with a mix of crawling. Rapidly, the wolves gave up crawling to focus entirely on walking. Once again, although we cannot determine exactly when behaviors of Stage 2 first emerged, we can nevertheless conclude that the wolves were already demonstrating behaviors of Stage 2 at the age of 23 days.

On Day 26, we observed secondary circular reactions in the wolves, which characterized Stage 3. These behaviors were directed towards external objects (social or physical) and produced a strong interest in the wolves. Biting another wolf, gnawing, pawing, and scratching were among the most frequent behaviors we observed (see Table 7.2). One characteristic of these behaviors is that they are voluntary: the wolves initiated these behaviors towards specific objects on their own; these behaviors were not simply the result of an accident or the mere proximity of another wolf. An example of a secondary circular reaction observed in the wolves is as follows: *Dharma bit Gordon's rear leg; Gordon ran away*; *Dharma then pursued Gordon by biting his leg again; Gordon ran away but Dharma sped up and bit Gordon once more.* During Stage 3, most of the wolves' behaviors were directed toward social objects, that is, their conspecifics, rather than towards non-social objects ($X^2_{(1)} = 20.24,\ p < 0.0001$).

Stage 4 of the SI period began on Day 50. The appearance of coordination between the different schemas of actions characterizes this stage. For example, Tilly grabbed a log with her mouth, ran away with it, and then began to chew it. In Stage 4, compared with the behaviors exhibited in Stage 3, the wolves were more inclined to explore physical objects, as illustrated by the fact that their number of interactions with inanimate objects was comparable to the number of social interactions with each other ($X^2_{(1)} = 0.02,\ p = 0.89$). For instance, in Week 10, a large cardboard box was introduced in the outdoor enclosure, and this captured the wolves' attention. Even if all three wolves simultaneously interacted with the box, there was no social interaction between the wolves, as all of their attention was directed towards the physical object. In Stage 4, it was also observed that the exploration of the environment (physical or social) by the wolves was characterized by the predominant use of the mouth: 88 % of the wolves' secondary circular behaviors involved the mouth. This observation highlights the fact that at this stage wolves explore the world by using their mouths much more than their paws ($X^2_{(1)} = 32.42,\ p < 0.01$).

We did not observe any behavior from Stage 5 or Stage 6 in our video recordings, which ended when the wolves were 76 and 79 days old. It was therefore concluded that tertiary circular reactions are either not present in the wolves' behavioral repertoire, or that these behaviors emerge solely after Week 11 of development.

7.2.5.2 Development of Object Permanence

In the visual pursuit tests, on the first and second days of testing (Day 24 and 25), the three wolves failed to follow the object up to its point of disappearance. On the third day of testing, two wolves (Tilly [Day 29] and Dharma [Day 32]) instantly reached Stage 3 of OP: they demonstrated the ability to follow the object during the entire trajectory and searched for the object behind themselves. However, one wolf (Gordon [Day 26]) solely reached Stage 2 of OP during his third day of testing: he was able to follow the object up to its point of disappearance but did not made any attempt to search behind his back. Gordon reached Stage 3 of OP on his fourth day of testing (Day 29). In summary, the wolves reached Stage 2 and Stage 3 of OP by the mean age of 29 and 30 days, respectively. Then, all wolves moved on the formal tests of OP, which started on Day 35.

Table 7.4 presents the individual performance of each wolf as a function of each test in each week. When a wolf failed a test, the same test was rerun the next week. However, on two occasions, the same wolf (Gordon) failed a test and was retested during the same week. As one can see in Fig. 7.1, the performance in the tests among the wolves was relatively homogenous: the wolves reached the same stages of OP at around the same age.

Most specifically, our wolves succeeded the partial occlusion problem (Test 1–Stage 3) at the mean age of 36 days. These first results are consistent with those obtained during Week 5 in the visual pursuit test. Success in the single visible displacement problem with initiation of movement by the wolves (Test 2–Stage 4a) was reached by the mean age of 53 days. Two wolves (Dharma and Gordon) passed Test 3 (Stage 4b) on their first attempt, but one wolf (Tilly) failed it,

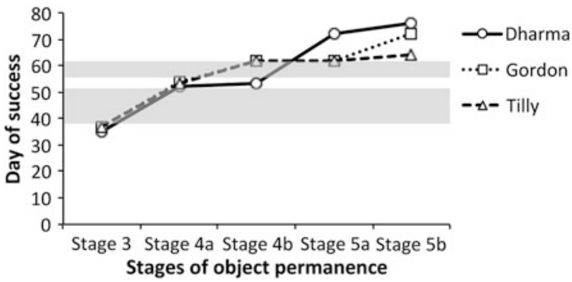

Fig. 7.1 Day of success for each wolf as a function of each stage of development of OP. The *two shaded areas* represent the periods of time during which the study was interrupted due to illness (Day 38–51) or the death of Devra (Day 56–61)

meaning that she may have committed the A-not-B error. However, out of the 4 errors she made on her first attempt in Test 3, Tilly searched four times behind box B and never behind box A (which was her target box in Tests 1–3). So, in spite of her failure on her first attempt in Test 3, we concluded with confidence that Tilly did not make any perseveration errors. Therefore, the wolves did not commit any A-not-B errors and they succeeded on Test 3 by the mean age of 59 days.

The wolves succeeded the sequential visible displacements (Test 4–Stage 5a) by the mean age of 65 days. By succeeding at these problems, the wolves demonstrated their first real understanding of the visible displacement of objects. Double visible displacements (Test 5–Stage 5b) were mastered by the mean age of 67 days, and triple visible displacements (Test 6–Stage 5b) were mastered by the mean age of 71 days. The result of the latter was judged as the date the wolves understandably mastered the visible displacement of objects.

In Test 7 (Stage 6a), two wolves failed the single invisible displacement problem and one wolf (Dharma) succeeded it. However, Dharma's performance in Test 7 was later discarded from the results. Indeed, both coders who reviewed the videotape of this particular test for this wolf agreed that methodological artefacts could explain her success. For instance, the target object occasionally came out of the transport device when the object was being moved to the target box, and, in one trial, the wolf was released by E2 before the end of the manipulation. On the other hand, when the manipulations were performed correctly (Gordon's and Tilly's Test 7), the wolves failed the problem and lost interest in the task, suggesting incomprehension of the invisible displacement problem. We therefore concluded that the wolves did not reach this stage of OP before the age of 12 weeks, that is, when we terminated the study.

7.2.5.3 Comparison with Domestic Dogs

As one of the objectives of the current study was to provide a comparison between dogs and wolves in regards to the development of their understanding of OP, we tentatively compared the performance of wolves in the OP tests with that observed by Gagnon and Doré (1994) in domestic dogs. As a reminder, Gagnon and Doré compared seven groups of dogs of different age, ranging from 4 weeks to

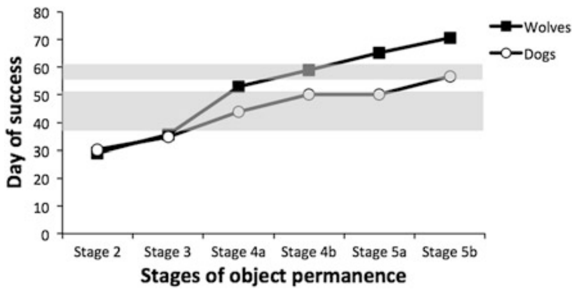

Fig. 7.2 Mean day of success for dogs (original data from Gagnon and Doré 1994) and wolves (current study) as a function of each stage of OP. The *two shaded areas* represent the two periods of time during which the study in wolves was interrupted. Data for Stage 2 were obtained by the visual pursuit tests and those for Stages 3–5b were obtained via the formal OP tests

9 months. In Gagnon and Doré (1994), when a group of a particular age failed to pass a test, the same test was administered to the next oldest group. Based on Gagnon and Doré's data in the visual pursuit tests and formal OP tests, we were able to identify the average age at which domestic dogs reached each stage of OP. Figure 7.2 illustrates the mean day of success of our three wolves (as a group) and of the dogs in Gagnon and Doré's study as a function of each stage of OP. As one can see, dogs' OP appears to develop at a faster pace than the one in wolves. In Stage 2 and 3, there were practically no differences between either species. From Stage 4a to 5b, however, the difference between dogs and wolves was striking: the dogs reached each stage at a much earlier age than the wolves. Depending on the stage, the difference ranged from 9 to 15 days.

However, given that the testing of OP in wolves had to be interrupted twice during the course of the current study, the results in wolves must be asterisked. We can suspect that the wolves would have been able to succeed some of the tests at an earlier age if they had been tested sooner during their development. To provide a better comparison between dogs' and wolves' development of OP, we estimated the mean age to which the wolves would have succeeded if testing had not beed delayed. To do so, we first calculated a differential ratio between the mean day to which dogs and wolves reached Stage 2 and Stage 3 (i.e. before the first interruption of the study). Then, we estimated the mean day of success of the wolves from Stages 3 to 5 by multiplying the mean day of success of dogs by this ratio. The result of this estimation is illustrated in Fig. 7.3. As one can see, if the wolves' testing had not been delayed, the wolves' results would have been quite similar to those of the dogs. However, we are plentifully conscious that this later approach is far from being perfect. Nevertheless, it helps to refine the results observed in wolves and illustrates that both species possibly have a very similar development of OP.

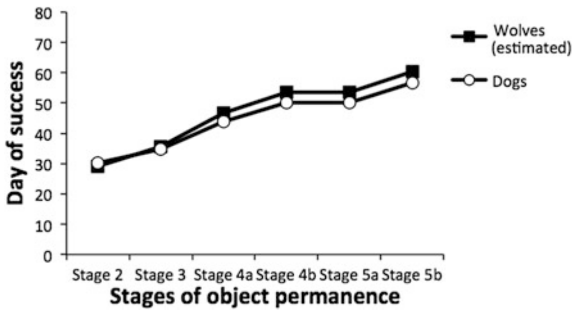

Fig. 7.3 Estimated mean day of success for wolves (to take into consideration the two periods of time during which the current study was interrupted) and the mean day of success for dogs (original data from Gagnon and Doré 1994) as a function of each stage of OP. Data for Stage 2 were obtained by the visual pursuit tests and those for Stages 3–5b were obtained via the formal OP tests

7.2.6 Discussion of Results

This study had two principal objectives. The first was to assess the development of OP in the gray wolf and compare it with the previous results found for the domestic dog (Gagnon and Doré 1994). The second was to observe the development of SI in the gray wolf and determine whether OP and SI develop at the same rate. To simplify the presentation, the results of the development of OP and SI are discussed separately. But first, a few methodological factors should be considered.

First of all, our small sample size reduces the certainty with which we can make generalized conclusions, and our results should be interpreted with caution. The same goes for our conclusions pertaining the exact moment in which wolves reached the different stages of OP, as the study was interrupted twice during a critical period of the wolves' cognitive and physical development. However, it should be noted that the wolves failed some OP tests that were administered after these two periods of interruption, suggesting that had testing not been suspended, they would not have reached that level of OP anyway. In addition, it is without a doubt that the small number of videos we were able to record limits the extent of the richness of the conclusions that can be made about the development of SI in wolves. For instance, we may have missed the appearance of some behaviors that characterized a particular stage. Consequently, the current study should be largely perceived as a pilot study, especially in regards to the timing at which the different stages of OP and SI occur. Nevertheless, we are confident that the conclusions regarding the general development of OP and SI are properly judged and well founded.

7.2.6.1 Development of Object Permanence

Overall, our results suggest that the development of OP in wolves is very similar to the one observed in domestic dogs (Gagnon and Doré 1994). It was observed that by the age of 4 or 5 weeks, both the dog and the wolf are capable of keeping track of an object that moves behind them. Around 5 weeks of age, both species succeed at Stage 3 problems. Thereafter, although it is difficult to establish with certitude the exact moment when wolf pups truly achieve Stage 4 and 5 of OP, the rate of development is mostly alike in both species. Our results also reveals that wolf pups, just like dog pups, do not commit the A-not-B error (Fiset and Plourde 2013; Gagnon and Doré 1992, 1994). In addition, between Weeks 8 and 10, dogs and wolves are both capable of succeeding at triple visible displacement problems. By the age of 12 weeks, however, both species fail invisible displacement problems.

The closeness of the rate at which dogs and wolves develop OP in the first stages can potentially be explained in part by the fact that the visual abilities of both species mature around the same age. In a study conducted by Lord (2012), dog pups and wolf pups were examined to determine the precise moment in which their olfactory, auditory, and visual senses fully develop. Their vision, which is critical in succeeding at OP tests, is only fully mature on Week 6 of life, which is also the time the dog and wolf pups in our study began demonstrating the capacity to truly locate disappearing objects. Prior to this time, neither species was capable of tracking and retrieving objects that had disappeared (Stage 3). This then poses the question of whether this failure was due to inability to see properly during their first weeks of life. Further testing is necessary to explore this idea.

In the current study, the 11-week-old wolves were unable to solve single invisible displacements. On the other hand, Gagnon and Doré (1994) reported that domestic dogs can resolve invisible displacement problems around the end of their first year of life. This introduces the possibility that wolves also reach Stage 6 of OP when they are around one year old. This would then explain the absence of this stage in our results, as our experiment was terminated by the end of Week 11 of life. This hypothesis is contradicted by the results of Fiset and Plourde (2013), who, using a spatial translation task administered to domestic dogs and adult wolves, demonstrated the incapability of either species to resolve invisible displacement problems. However, it should be noted that Fiset and Plourde (2013), in contrast with Gagnon and Doré (1994), did not use the Piagetian invisible-displacement problem. Given that translational problems are perceived as more difficult than those developed by Piaget (Fiset and Plourde 2013), it still remains possible that the adult wolves could solve the latter. However, recent work (Collier-Baker et al. 2004; Fiset and LeBlanc 2007) rejected the conclusion that adult dogs may solve Piagetian invisible displacement problems. These authors found that dogs primarily search as a function of the position of the displacement device and that, to a lesser extent, the presence of an experimenter behind the apparatus increases success in invisible displacement problems. Based on these last observations, we do not believe that adult wolves are capable of solving Piagetian invisible displacement problems. Nevertheless, this hypothesis remains to be confirmed empirically.

7.2.6.2 Development of Sensorimotor Intelligence

In investigating the development of SI in wolves, we can conclude that Stage 1 and 2 are both attained before the age of 23 days, Stage 3 is acquired during the fourth week of life, and Stage 4 is reached during the eighth. However, our observations did not allow us to detect any behaviors of Stage 5 or 6 in wolves by the end of Week 11 of life, when our study was terminated. This last conclusion contrasts with that of Frank and Frank (1985) who suggested that 10-week-old wolves may reach Stage 5, and possibly Stage 6, of SI. How can we explain the discrepancy between our study and the one performed by Frank and Frank? First, it is possible—like Dumas and Doré (1991) argued about domestic cats, which also do not reach Stage 5 of SI—that this is simply due to the complexity of such behaviors, and that observing these behaviors during natural interactions with the environment is very rare. Secondly, our study, similar to the approach used by Piaget (1954) with children, relied exclusively on behavioral observations to determine the stages of SI reached by the wolves. Contrarily, Frank and Frank created an experimental procedure in which young wolves had to perform tasks of increasing complexity to extract a food dish from a box. They then interpreted the behaviors of the wolves following criteria for SI. However, as pointed out earlier, in Frank and Frank, the wolves may have used strategies from Stage 3 to resolve problems that were supposed to be Stage 5, rendering their results difficult to interpret. We are therefore confident that the current study reinforces the conclusion that wolves' SI is limited to Stage 4, which is similar to what was observed by Frank and Frank in domestic dogs, supporting the hypothesis that all canine species present a similar development of SI.

Based on our observations, several general conclusions on the development of SI in wolves can be made. Firstly, the role of secondary circular reactions in young wolves seems to be a dominant factor in their development of SI. Behaviors like biting other wolves or objects, pawing or kicking, scratching the ground, wrestling, and tugging objects, were displayed with great frequency. Primary circular reactions, in contrast, were barely present, only being exhibited during activities like moving around, or gregarious behaviors such as snuggling. Even at a very young age, the pups seemed significantly more oriented towards external objects. This interest in the external world and the pups' tendency towards secondary circular reactions can be explained by the fact that wolves demonstrate an early development of motor coordination (Lord 2012). This early acquisition of locomotor skills, which emerges by the end of the second week of life, allows wolves to explore their environment, most likely allowing them to develop an intrigue for external features. By comparison, locomotor development in dogs emerges by Week 3 of age and is fully functional by Week 4 (Lord 2012). However, since no one has yet investigated the development of SI in dogs, it still remains to determine the exact role of locomotion on the development of SI in canines.

In the current study, it was also noted that the majority of secondary circular reactions, despite their large number, were expressed principally through the wolf pups' mouths. This link between the dominance of behaviors issued through the mouth and secondary circular reactions is characteristic of the third stage of sensorimotor development. In fact, in children, the third stage of the sensorimotor period is defined by the ability to grip objects, which is also first expressed through the mouth. Moreover, in wolves, the third stage of SI is reached before the third stage of OP, which is unlike in children, where the development of these two concepts occurs in a relatively synchronized manner. We hypothesis that the early development of mobility and grip—an ability demonstrated by the use of the mouth in wolves—favors the rapid development of the first three stages of SI, which leads to asynchrony between OP and SI development in wolves. Interestingly, this asynchrony in the wolf is very similar to that observed in the domestic cat (Dumas and Doré 1991), another species that acquires mobility and grip at an early age.

Finally, it was remarked that during their first interactions with the external world (Stage 3), the wolves predominantly oriented their behaviors towards their conspecifics, supporting observations by Lord (2012), who found that the wolf's period of socialization begins at 2 weeks of age. Interestingly, the wolves' constant interactions with each other may explain, in part, their development of OP. Indeed, since wolves are highly mobile and move around, they frequently disappear from each other's sight. From this we can postulate that they gradually learn or acquire the ability to keep track of their conspecifics by developing the mental capacity to remember where they have disappeared in the surrounding environment. Future work should explore the possible link between the development of OP and wolves' tendency to interact with mobile social objects.

7.3 Conclusion

In conclusion, the current study suggests that both domestic dogs and gray wolves share a similar evolutionary past that, over several thousand years, shaped their ontogenetic development of OP (and possibly SI) in a similar way. For instance, both species are gregarious and in the wild chase prey for survival. Since these skills necessitate the ability to keep track of moving objects, this fact potentially explains why both dogs and wolves present a similar development of OP. However, to acquire a more complete understanding on this question, future studies must include other canine species, as well as increase the sample size of species. In addition, the current research provides a first description of the ontogenetic development of SI in wolves by using criteria from Piaget's theory of cognitive development, suggesting that OP and SI in canines develop in an unsynchronized manner. A systematic comparison between dog and wolf development of SI and OP, however, is needed to further understand the reasons underlying this unbalanced relationship, especially in regards to the development of canines' senses.

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