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Author
Wechsler, Beat

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Three Levels of Consciousness: A Pattern in Phylogeny and Human Ontogeny

Beat Wechsler

Federal Food Safety and Veterinary Office, Centre for Proper Housing of Ruminants and Pigs, Switzerland

Investigations in the cognitive abilities of different animal species and children at different ages have revealed that consciousness comes in degrees. In this review, I will first address four cognitive abilities that are important to discriminate levels of consciousness: mirror self-recognition, theory of mind, mental time travel, and the capacity to entertain secondary representations. I will then examine putative relations between these abilities and assign them to three levels of consciousness (anoetic, noetic, autonoetic). Finally, I will discuss the implications of differences in consciousness for the understanding of behavioral organization in animals and humans and for animal welfare science. I will argue that, on one hand, implicit behavioral rules may account for results obtained in research on theory of mind and mental time travel abilities in animals and children. On the other hand, secondary representations may be the key to explain behaviors based on semantic memory as well as semantic future planning abilities observed in great apes and young children. These considerations are in accordance with the view that an explicit theory of mind and a continuous self through time are unique to humans.

Keywords: consciousness, self-awareness, theory of mind, mental time travel, animal welfare

Over the last 20 years, much progress has been made in animal cognition research. Experimental studies have shown differences in mirror self-recognition between animal species, and a variety of species have been tested for cognitive abilities indicative of a theory of mind. Moreover, episodic-like memory and planning for the future have been explored in different animal species. In parallel, the development of cognitive abilities in human ontogeny has been studied extensively. Studies have examined behavioral and cognitive abilities emerging at the same time as mirror self-recognition, implicit and explicit theory of mind abilities in infants and preschool children, and the development of episodic memory and future thinking in early childhood. As elaborated in this review, there is a general pattern across these studies, in that cognitive abilities in humans and nonhuman animals can be assigned to three levels of consciousness (anoetic, noetic, autonoetic), differentiating between evolutionary and ontogenetic stages.

Research on cognitive abilities in children and nonhuman animals is carried out in both developmental and comparative psychology. Typically, a researcher is an expert in a defined research topic, such as theory-of-mind development in human infants or behavioral indicators of episodic-like memory in animals. Accordingly, review papers often focus on a specific cognitive ability, such as theory of mind (e.g., Apperly & Butterfill, 2009; Burge, 2018; Call & Tomasello, 2008; Penn & Povinelli,

Please send correspondence to Beat Wechsler, Centre for Proper Housing of Ruminants and Pigs, Agroscope Taenikon, Switzerland. (Email:beat.wechsler@agroscope.admin.ch)
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2007; Scott & Baillargeon, 2017), mental time travel (e.g., Cheke & Clayton, 2010; Martin-Ordas & Call, 2013; Roberts & Feeney, 2009; Suddendorf & Corballis, 2007; Tulving, 2005) or self-awareness (e.g., Bard, Todd, Bernier, Love, & Leavens, 2006; Boyle, 2017; Gallup & Anderson, 2018; Schilhab, 2004). In this review, I will take a broader view and address four research topics that are related to human and animal consciousness, namely mirror self-recognition, theory of mind, mental time travel, and the capacity to entertain secondary representations (i.e., section "Cognitive Abilities"). I will discuss studies investigating the developmental trajectory of these cognitive abilities in human ontogeny and studies aiming to provide evidence for these abilities in nonhuman animals. Furthermore, I will examine putative relations between these abilities (i.e., section "Relations Between Cognitive Abilities") and assign them to three levels of consciousness (i.e., section "Patterns in Phylogeny and Human Ontogeny"). Finally, I will explore the implications of the different levels of consciousness for understanding behavioral organization in animals and humans and for animal welfare science.

Cognitive Abilities

Mirror Self-recognition

To test for the ability of mirror self-recognition, children and animals have been marked with dye or stickers on their face or head as well as on additional otherwise nonvisible body parts. By comparing the responses in test and control sessions with and without a mirror, respectively, it is possible to assess whether the subject paid attention to the mark (Bard et al., 2006; Gallup, 1970). In response to the mirror, different types of behavior can be observed: mirror-directed behaviors (e.g., touch, play, attack), contingent movements (defined as movement of the head or the body while visually following the movements in the mirror), mirror-guided body-directed behavior (e.g., touching or visually inspecting parts of the body), and mirror-guided mark-directed behavior (Lin, Bard, & Anderson, 1992). To differentiate mark-directed behavior from accidental touching of the face or body, the frequency of touches on the mark and on comparable unmarked facial regions should be considered (Povinelli et al., 1997).

Children and animals using mirror reflection to respond to the mark on the face, head, or body are assumed to be capable of mirror self-recognition. In human infants, mirror self-recognition emerges between 18 and 21 months (Amsterdam, 1972; Nielsen & Dissanayake, 2004) and is shown by a majority of infants by 24 months of age (Anderson, 1984). With regard to nonhuman animals, the evidence for mirror self-recognition is controversial. Several studies have shown that great apes pass the mark test, whereas there is no compelling evidence that monkeys are capable of mirror self-recognition (Anderson & Gallup, 2015). Plotnik, de Waal, and Reiss (2006) reported that one of three tested Asian elephants increased head touching during or right after mirror exposure and that touches came in contact with or close to the visible mark on one side of the head, but not to a "sham" mark on the other side of the head. However, Povinelli (1989) failed to witness self-recognition in two Asian elephants exposed to a mirror. With dolphins, Reiss and Marino (2001) found that two individuals exposed to reflective surfaces “demonstrated responses consistent with the use of the mirror to investigate marked parts of the body” (p. 5937). With birds, Prior, Schwarz, and Gunturkun (2008) reported that three out of five magpies tested using a mark test “showed at least one instance of spontaneous self-directed behavior” (p. 1644), whereas Soler, Perez-Contreras, and Peralta-Sanchez (2014), following the experimental protocol described by Prior et al. (2008), found no evidence of self-recognition in jackdaws. However, the results of the study with jackdaws suggested that the birds were able to tactilely perceive the self-adhesive stickers used as marks on the throat feathers. Finally, Clary and Kelly (2016) observed that 1 out of 10 Clark’s nutcrackers tested showed more actions to the region on the throat feathers marked with a red dot when exposed to a mirror than during control conditions, concluding that this bird may have shown evidence of self-recognition.

Theory of Mind

In their seminal paper, Premack and Woodruff (1978) asked whether chimpanzees have a theory of mind. They had observed that Sarah, a 14-year-old chimpanzee born in the wild and raised in a laboratory since she was 1 year old, was able to select from a pair of photographs the one that matched a problem presented in a video sequence showing a human actor struggling with the problem. She made a correct choice in 21 out of 24 trials with a variety of problems, indicating that she understood the actor’s purpose and could choose alternatives compatible with that problem. To do so, she possibly had to impute a mental state to the human actor, the purpose of an action that would solve the problem he was struggling with, thus showing that she possessed a theory of mind.

Thirty years later, Call and Tomasello (2008) reviewed the evidence and concluded that “there is solid evidence from several different experimental paradigms that chimpanzees understand the goals and intentions of others, as well as the perception and knowledge of others” (p. 187). For example, chimpanzees, as well as all other great ape species, follow gaze to distant locations and around barriers (Bräuer, Call, & Tomasello, 2005). They are able to distinguish “unwilling” from “unable,” producing more behaviors commonly used by chimpanzees to request food from humans when an experimenter is unwilling versus unable (but willing) to give them food (Call, Hare, Carpenter, & Tomasello, 2004). In competitive situations, chimpanzees will pick the food that a dominant conspecific cannot see because of a barrier, thus inferring what the competitor does and does not see (Hare, Call, Agnetta, & Tomasello, 2000). Also, subordinate chimpanzees can consider whether dominant conspecifics could witness the baiting procedure in a food competition test; they preferentially approach and retrieve the food that dominants had not seen hidden (Hare, Call, & Tomasello, 2001).

Call and Tomasello (2008) compared chimpanzees’ and human infants’ understanding of goals and intentions as well as perception and knowledge. In many of the tasks, the performance of chimpanzees was similar to that observed in infants;

however, at that time, there was no experimental evidence that chimpanzees recognized that an agent can hold a false belief. In a comparative study, Kaminski, Call, and Tomasello (2008) had carried out a nonverbal false-belief task with both chimpanzees and 6-year-old children. Using an experimental paradigm involving competition with a conspecific, they found that the chimpanzees understood knowledge-ignorance but not false belief, whereas the children understood both of these mental states. However, Krupenye, Kano, Hirata, Call, and Tomasello (2016), using an anticipatory looking test originally developed for human infants, found that chimpanzees, bonobos, and orangutans reliably looked in anticipation of an agent acting on a location where he falsely believed an object to be. Similarly, Buttelmann, Buttelmann, Carpenter, Call, and Tomasello (2017) showed that great apes as a group, including chimpanzees, bonobos, and orangutans, distinguished between true and false beliefs in their helping behavior during an interactive helping task. These results suggest that great apes also operate with an understanding of false beliefs, at least on an implicit level. In experiments with human infants, implicit understanding of false belief was found in 15-month-olds in a violation-of-expectation paradigm (Onishi & Baillargeon, 2005) and in 18-month-olds in an interactive helping task (Buttelmann, Carpenter, & Tomasello, 2009).

Mental Time Travel

Clayton and Dickinson (1998) reported that scrub jays demonstrated “memory of where and when particular food items were cached, thereby fulfilling the behavioral criteria for episodic-like memory in nonhuman animals” (p. 272). Since then, it has been debated whether animals are “stuck in time” (Roberts, 2002). Basically, the question is whether animals are really able to remember past episodes (episodic memory) or just know what has happened in the past (semantic memory). The distinction between these two types of memory was introduced by Tulving (1985, 2001), differentiating between *autonoetic* and *noetic* awareness of the past, the former describing “the experiential ‘flavor’ of remembering, or recollection,” and the latter describing “the conscious state that accompanies thinking about (knowing) the world” (Tulving, 2002, p. 4).

The problem of distinguishing between semantic and episodic memory is well illustrated by the study of Menzel (1999). He had reported that Panzee, a female chimpanzee, was able to guide a person to the location where she witnessed an experimenter hide an object in the woods outside her outdoor enclosure up to 16 hours ago. She did so by catching the person's attention while in the indoor enclosure, pointing outdoors, going outdoors and, when followed by the person, pointing toward the object and vocalizing until the person found the object. Menzel entitled his publication “Unprompted recall and reporting of hidden objects by a chimpanzee after extended delays.” However, Suddendorf and Corballis (2007) queried whether this study provided evidence of episodic memory and stated that “although this shows that Panzee knew where the food was, it does not prove that she remembered the hiding event itself” (p. 303).

When nonhuman animals demonstrate memory of what occurred where and when, this cognitive ability is usually labelled as “episodic-like” memory (Clayton & Dickinson, 1998) or what-where-when memory (Cheke & Clayton, 2010) because the phenomenological experience of this type of memory (i.e., autonoetic consciousness; Tulving, 1985, 2001) is of a private nature and thus cannot be shown to exist (Suddendorf & Busby, 2003). Over the years, what-where-when memory has been identified in many species, such as rats (Babb & Crystal, 2005), meadow voles (Ferkin, Combs, delBarco-Trillo, Pierce, & Franklin, 2008), and black-capped chickadees (Feeney, Roberts, & Sherry, 2009). Moreover, it was found that when no temporal information is available, animals use contextual cues to differentiate between similar memories, suggesting that “the concept of what-where-when should be broadened in order to include any contextual cue that defines a specific occasion in which an event occurred” (Martin-Ordas & Call, 2013, p. 5). Consequently, it was proposed to replace what-where-when memory by the more encompassing term what-where-which memory (Eacott & Easton, 2010). Again, studies with a variety of species, such as rats (Panoz-Brown et al., 2016), Yucatan minipigs (Kouwenberg, Walsh, Morgan, & Martin, 2009), and zebrafish (Hamilton et al., 2016), have shown that nonhuman animals are capable of discriminating between similar memories, taking into account the context in which the event occurred. With great apes, it was found that they are able to recall events that happened in a specific tool-finding or food-hiding event after delays as long as 50 weeks (Lewis, Call, & Berntsen, 2017a; Martin-Ordas, Berntsen, & Call, 2013), and Lewis, Call, and Berntsen (2017b) showed that distinctiveness of a past event enhanced the apes’ long-term memory. Furthermore, Dekleva, Dufour, de Vries, Spruijt, and Sterck (2011) reported that chimpanzees failed a what-where-when task when tested with a food-caching paradigm but found rewards by using a simple location-based association strategy, based on the experienced reward quality of four locations baited in the course of the study. Finally, the use of episodic-like memory in a foraging context is not limited to great apes and to experiments with captive animals. Noser and Byrne (2015) reported that a wild chacma baboon remembered single foraging episodes and that this ability prevented him from revisiting already depleted food sites. As summarized by Martin-Ordas and Call (2013):

> Episodic memory might specifically be about discriminating complex events from one another based on the arrangements of items on a particular occasion. The occasion may be defined by a number of cues, but crucially they do not have to be temporal in nature. (p. 7)

In humans, mental time travel covers the past as well as the future, and it has been hypothesized that the ultimate evolutionary advantage of this cognitive ability lies with the capacity to access the future (Schacter, Addis, & Buckner, 2007; Suddendorf & Corballis, 2007). To investigate whether nonhuman animals have the capacity for episodic future-thinking, Tulving (2005) proposed the “spoon test.” In this test, subjects have to anticipate that they will require a tool in a future situation (e.g., a spoon to eat chocolate pudding) and should acquire the tool earlier and carry it to the place where it is needed to solve the task. In studies with bonobos, orangutans, and chimpanzees, Mulcahy and Call (2006) and Osvath and Osvath (2008) observed that apes saved tools for future use. Contrary to this, macaques and capuchin monkeys did not spontaneously transport tools for future use but could be trained to do so (Bourjade, Thierry, Call, & Dufour, 2012; Dekleva, van den Berg, Spruijt, & Sterck, 2012; Judge & Bruno, 2012).

Secondary Representations

In children, pretend play is considered to be an indicator of their ability to form secondary representations (Leslie, 1987). By having this ability, they are, for example, able to use a banana to make an imaginary phone call. They can consider the banana a telephone although, as a primary representation, it is still a banana. They have a secondary representation of a telephone that is decoupled from primary representations and can therefore be used in pretend play. Interestingly, pretend play emerges towards the middle of the second year and in parallel with two other cognitive abilities, synchronic imitation and mirror self-recognition (Nielsen & Dissanayake, 2004). In synchronic imitation tasks, an experimenter models an action with an object, and it is recorded whether the child imitates the action of the experimenter using a duplicate of his or her object. The ability to do so may rely on the psychological mechanism necessary for pretend play; the child is able to have a secondary representation of the action performed by the experimenter and/or the goal of his behavior and to copy the observed behavior pattern to attend the same goal. Likewise, children showing mirror self-recognition are able to correspond the picture in the mirror to a secondary representation of the self (Asendorpf & Baudonnière, 1993; Bard et al., 2006; Bischof-Köhler, 2012).

In their experimental study, Nielsen and Dissanayake (2004) did a detailed analysis of the patterns of emergence of synchronic imitation, pretend play, and mirror self-recognition in infants. They reported that the three skills emerged between 18 and 21 months and followed similar developmental trajectories. Moreover, they found that none these skills were a developmental precursor to the emergence of the other skills and that the majority of infants took from 3 to 6 months to show all three skills once they had shown one skill. These skills thus seem to rely on the maturation of a common underlying mechanism, the capacity for secondary representation.

As great apes have been shown to be able to recognize themselves in the mirror (Anderson & Gallup, 2015; Povinelli et al., 1997), they may also have the capacity for secondary representation. In their review, Suddendorf and Whiten (2001) described additional cognitive abilities observed in great apes that fit this hypothesis. They mentioned, for example, that home-reared members of all great ape species have been reported to treat dolls as if these were animate characters and that language-trained great apes are able to interpret and make use of human symbols. Taking information about representational skills in both children and animals into account, they summarized that there is a “cluster of mental accomplishments in great apes that is very similar to that observed in 2-year-old humans” (p. 629).

Relations Between Cognitive Abilities

Consciousness comes in degrees, as do self-awareness, theory of mind abilities, and mental time travel abilities. Having searched the scientific literature on animal and human cognition, I suggest that progress in these abilities, during both phylogeny and human ontogeny, can be described adequately by differentiating between three levels of consciousness. Subsequently, I will introduce these levels before I address the relation between theory of mind and mental time travel abilities as well as between semantic memory and secondary representations.

Three Levels of Consciousness

In their meta-analysis, Wellman, Cross, and Watson (2001) found that children typically pass standard verbal false-belief tasks at 4 years and older. Similarly, it is only at the age of 4 years that children have acquired an awareness of the self as continuous through subjective time (Povinelli, 2001) and are able to mentally construct specific future events (Suddendorf & Redshaw, 2013). Thus, they do have autonoetic awareness of their experiences “in the continuity of subjectively apprehended time that extends both backward into the past in the form of ‘remembering’ and forward into the future, in the form of ‘thinking about’ or imagining or ‘planning for’ the future” (Tulving, 2001, p. 1506). They are also able to apply the theory of mind to their own mental states (Fonagy, Gergely, Jurist, & Target, 2002, p. 27), introspecting their self from a third-person perspective. Theory of mind ability is therefore linked to mental time travel; it is the introspective self who is capable of episodic memories and episodic future thinking. As Tulving (2002, p. 2) wrote: “mental time travel requires a traveler. No traveler, no traveling.”

Already in the middle of the second year, however, children have acquired noetic awareness in that they are aware of “the existence of the world and objects, events, and other regularities in it, independently of self, autonoetic awareness and (subjective) time” (Tulving, 2001, p. 1506). This level of consciousness is characterized by the capacity to entertain secondary representations, indicated by the emergence of synchronic imitation, pretend play, and mirror self-recognition between 18 and 21 months of age (Nielsen & Dissanayake, 2004). At that age, children do have a secondary representation of the self, which Howe, Courage, and Edison (2003, p. 480) described as “a new organizer of information and experiences” that “facilitates the grouping and personalization of memories for events.” At that level of consciousness, however, these memories are semantic and not episodic (Tulving, 1985), as the children do not yet have the capacity for mental time travel. Nevertheless, 3-year-olds are able to report on past events (Gopnik & Slaughter, 1991). Similarly, they do not yet have a mature theory of mind but are able to infer what others see and feel (Wellman, Phillips, & Rodriguez, 2000).

Tulving (1985) termed a third level of consciousness as anoetic and characterized it as “temporally and spatially bound to the current situation” (p. 3). Organisms possessing anoetic consciousness lack the capacity to entertain secondary representations. In line with this, Vandekerckhove (2009, p. 18) described anoetic consciousness “as a stream of pre-reflective procedural sensory affective and visceral consciousness.” Studies into blindsight suggest that macaques do have primary representations of visual stimuli (Cowey & Stoerig, 1995), and it is plausible to assume that this may also be true for other types of sensory input, not only in monkeys but also generally in mammals and vertebrates, given the homology of their sensory and neural systems. Primary representations are likely to result also in implicit awareness of a self in interaction with the environment, labelled as *anoetic self-experience* by Vandekerckhove (2009). To describe the self in early human ontogeny, William James (1961) distinguished between the “I” and the “me”, the former being a kind of unreflected self-sensing, with the self as the subject of experience “embedded in carrying out activities, in producing effects, and in having sensations” (Bischof-Köhler, 2012, p. 43), and the latter being a secondary representation of this subject that is recognized in the mirror once the child possesses noetic consciousness.

Relation Between Theory of Mind and Mental Time Travel Abilities

At around 4 years of age, children typically start to pass explicit verbal false-belief tasks (Grosse Wiesmann, Friederici, Singer, & Steinbeis, 2017; Rakoczy, 2017; Scott & Baillargeon, 2017), which coincides with the emergence of the capacity for mental time travel (Atance & Meltzoff, 2005; Busby & Suddendorf, 2005; Russell, Alexis, & Clayton, 2010; Suddendorf & Busby, 2005; Ünal & Hohenberger, 2017). In support of a possible link between theory-of-mind development and mental time travel ability, Perner, Kloo, and Gornik (2007) showed that growing theory-of-mind understanding went along with enhanced episodic memory in 3.5- to 6.5-year-old children. With regard to episodic future thinking, Ford, Driscoll, Shum, and Macaulay (2012) reported that theory of mind, as gauged by false-belief tests, predicted 4- to 6-year-olds’ success on measures of prospective memory.

Both explicit verbal false-belief and the capacity for mental time travel are significantly related to children’s linguistic abilities (Grosse Wiesmann et al., 2017; Milligan, Astington, & Dack, 2007; Ünal & Hohenberger, 2017). In addition, there is controversial evidence concerning the relation between theory of mind as well as mental time travel abilities and executive function, an umbrella term for a set of cognitive abilities including inhibition, working memory, planning, cognitive flexibility, and generativity that allow an individual to solve a problem or accomplish a goal (Hanson, Atance, & Paluck, 2014). In a meta-analysis of studies done with 3- to 6-year-old children, for example, Devine and Hughes (2014) found a moderate association between executive function and false-belief understanding. Grosse Wiesmann et al. (2017) tested 3- and 4-year-olds with a battery of explicit and implicit false belief tasks and demonstrated that the former tasks correlated with executive function, whereas the latter tasks did not. Moreover, Ünal and Hohenberger (2017) reported that executive function, after controlling for age, predicted the performance of 3- to 5-year-olds in a what-where-when task to measure episodic memory but not in a future prediction task to measure episodic future thinking. Finally, Hanson et al. (2014) found that, after controlling for age and language ability, the performance of 3- to 5-year-old children in executive function tasks was not related to their performance in a variety of theory-of-mind and episodic-foresight tasks. Possibly, the results of these studies are inconsistent because executive function is not a uniform concept. Therefore, different tasks used to measure executive function may require different cognitive abilities associated with either noetic or autonoetic consciousness.

Also at around 4 years of age, children acquire Level-2 perspective-taking abilities and understand that "an object simultaneously visible to both the self and the other person may nonetheless give rise to different visual impressions or experiences in the two if their viewing circumstances differ" (Flavell, Everett, Croft, & Flavell, 1981, p. 99). Furthermore, between the ages of 3 and 5, related to the development of false-belief reasoning, children acquire the capacity to understand identity statements such as "Mr. Müller is the firefighter" (Perner, Mauer, & Hildenbrand, 2011) and to appreciate the difference between appearance and reality, enabling them to understand that "this looks like X but really is Y" (Gopnik & Astington, 1988, p. 28). These two capacities also build on the ability to address an issue from two points of view.

Bischof-Köhler and Bischof (2007) argued that the synchronous development of theory of mind and mental time travel in children is due to the emergence of a shared competence, the ability to become aware of frames of reference and to simultaneously represent contradicting frames of reference. With this ability, children understand that another person has a different frame of reference and therefore holds a different perspective on the world. They are also able to recognize that others have a different state of knowledge and may hold false beliefs. Similarly, they understand that their self is continuous across different temporal coordinates in the past and the future. In line with this, Tomasello and Moll (2013) hypothesized that great apes do not pass false-belief tasks, because "understanding a belief as false involves some kind of conflict - a conflict in which the most salient alternative, namely the agent's own knowledge of what is the case, must be suppressed or ignored" (p. 83). This interpretation is not questioned by the results of recent studies showing implicit false-belief understanding in great apes (Buttelmann et al., 2017; Krupenye et al., 2016) because implicit false-belief tasks do not require autonoetic consciousness and can be solved without representing contradicting frames of reference. This issue is further discussed in the section "Implicit and explicit theory of mind abilities."

Relation Between Semantic Memory and Secondary Representations

The capacity for secondary representation enables 2-year-old children to think of and talk about a "me" as the center of perception and action. They use the personal pronouns *me*, *my*, or *mine* to refer to this "me" (Lewis & Ramsay, 2004), and, in everyday interaction with them, it is not easily evident that the "me" is different from the introspective self that only emerges around 4 years of age. Even though the capacity for mental time travel is still lacking, the secondary representation of the self enables children to assign past events and future actions to this "me." However, the "me" is not yet able to mentally travel in time, neither backward nor forward. Consequently, when 3-year-olds report what they did yesterday and what they are going to do tomorrow (Suddendorf, 2010), they may do so by generating well-known scripts or routines (Martin-Ordas, Atance, & Caza, 2014) rather than projecting themselves (a self that exists through time) back into the past and forward into the future. The relationship between semantic knowledge of the world and 3-year-olds' goal-directed behavior and conversations about past or future events is further elaborated in the sections “Goal-directed behavior and episodic future planning” and “What is uniquely human?”.

In parallel to the “me”, 2-year-olds are able to have secondary representations of the “other” and to show empathy to persons. In a study with 16- to 24-month-olds, Bischof-Köhler (2012) found that all empathic children, showing concern and compassion with a playmate that had accidentally broken a spoon or a teddy, recognized themselves in the mirror. The capacity for empathy enables children to assign emotional and motivational states to the “you” before they acquire an explicit theory of mind at the age of around 4 years; they are not yet able to consider “What would I feel if I were in the playmate's situation?” (Bischof-Köhler, 2012, p. 44). Likewise, Lillard (1993) reviewed studies on children's pretend play skills and concluded that early sociodramatic play may involve the execution of scripted routines, rather than imagining others' mental representations.

Possibly, the ability to form secondary representations is crucial for the excellent performance of great apes observed in a variety of cognitive tasks. For example, Sayers and Menzel (2012) demonstrated that chimpanzees could memorize ten locations where transparent bags filled with almonds were hidden in a large wooded test area in addition to the quantity of almonds in a given bag. After observing foods being hidden, they were able to direct naïve humans to the reward locations, such that the persons recovered large quantities of almonds before the smaller quantities. Furthermore, Beran, Perdue, Bramlett, Menzel, and Evans (2012) observed that a female chimpanzee, at the end of a 30-min period of foraging on scattered food in an outdoor enclosure, consistently remembered to retrieve a lexigram token symbolizing a food item she could receive in exchange for the token upon return to the indoor enclosure. To do so, she had to search the correct token among eight face-down lexigram tokens distributed throughout the outdoor yard. Finally, Premack and Premack (1972) reported that a chimpanzee who was trained to use plastic word symbols for nouns and adjectives attributed symbols representing characteristics of an apple to not only a real apple but also to a blue plastic triangle that was the word for apple. As explained in the section “Self-awareness associated with mirror self-recognition,” passing the mark test indicates that great apes may have a secondary representation of the “me.”

Patterns in Phylogeny and Human Ontogeny

In this section, I will link mirror self-recognition, theory of mind abilities, and mental time travel abilities to the levels of consciousness described above (anoetic,

noetic, autonoetic). More specifically, I will address various cognitive tasks that have been used in studies with both nonhuman animals and children. Table 1 gives an overview of these tasks and their assignment to the three levels of consciousness. I will focus on topics that are highly debated in the current literature on animal and human cognition: the role of behavioral rules to explain cognitive abilities, mirror self-recognition in animal species other than great apes, the distinction between implicit and explicit theory of mind abilities, and the contribution of semantic and episodic future planning to the interpretation of tool use in great apes. Moreover, I will address cognitive abilities that are likely to be uniquely human and discuss implications of the three levels of consciousness for animal welfare.

Table 1

Cognitive Abilities in Humans and Nonhuman Animals at Different Levels of Consciousness

Level of consciousness	Self-awareness abilities	Theory-of-mind abilities	Mental time travel abilities
Anoetic	Contingent movements in front of the mirror	Gaze following	Procedural memory
	Mirror-guided self-directed behavior	Distinguish “unwilling” from “unable”	Ability to build up expectations based on past events
	Body awareness	Understanding of the pointing gesture	Ability to monitor past cognitive activities (metacognition)
	Implicit sense of agency	Attribute knowledge and ignorance to others	Episodic-like memory (what where when / what where which)
		Level-1 perspective-taking Deferred imitation Rational imitation Refer to absent entities Implicit false-belief understanding	
Noetic	Mirror self-recognition Secondary representation of the self (the “me”)	Synchronic imitation Secondary representation of the other (the “you”)	Semantic memory Explicit memory of what happened to the “me” Secondary representation of goal states Secondary representation of goal-directed behaviors Semantic prospection
Autonoetic	Continuous self through time	Level-2 perspective-taking	Episodic memory Autobiographical memory Episodic future thinking
	Introspective self-awareness	Explicit false-belief understanding	

Behavioral Rules

When studies investigating theory of mind abilities in great apes were published, it was questioned whether the results provided clear evidence of mind-reading in animals. As an alternative, applying the principle of parsimony (Heyes, 1998; Shettleworth, 2010), it was suggested that the results can also be explained by inferring that the apes are capable of behavior-reading. Concerning the study of Hare et al. (2001), for example, Povinelli and Vonk (2003) pointed out that the behavior of the subordinate chimpanzee might result from a simple strategy: “Don’t go after food if a dominant who is present has oriented towards it” (p. 159). If the subordinate chimpanzee solves the task using this behavioral rule, the additional claim that he adopted this strategy because he “understood that ‘the dominant knows where the food is located’ is intuitively appealing but causally superfluous” (Penn & Povinelli, 2007, p. 735). In line with such thinking, the behavior-reading interpretation is supported by the results of studies using the competitive food paradigm developed by Hare et al. (2001) with various animal species. It was found that long-tailed macaques (Overduin-de Vries, Spruijt, & Sterck, 2014), common marmosets (Burkart & Heschl, 2007) and domestic goats (Kaminski, Call, & Tomasello, 2006) preferred the piece of food that was hidden from the dominant’s view.

Over the years, many studies revealed that animals other than great apes were successful in different theory-of-mind tasks. For example, gaze following was observed in domestic goats (Kaminski, Riedel, Call, & Tomasello, 2005) and red-footed tortoises (Wilkinson, Mandl, Bugnyar, & Huber, 2010). Moreover, Tonkean macaques (Canteloup & Meunier, 2017), Capuchin monkeys (Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009), and grey parrots (Peron, Rat-Fischer, Nagle, & Bovet, 2010) were shown to understand human intentional actions in experiments using the “unwilling” versus “unable” paradigm. Finally, great apes (Mulcahy & Hedge, 2012), African elephants (Smet & Byrne, 2014) and domestic pigs (Nawroth, Ebersbach, & von Borell, 2014) used human pointing cues to find hidden food.

In support of the hypothesis that some theory-of-mind abilities observed in great apes and other animal species could be based on behavioral rules, it was found that human infants, markedly younger than 18 months of age and thus not yet capable of mirror self-recognition, are able to solve such tasks. Infants as young as 8 months can infer the presence of hidden objects from referential gaze information (Csibra & Volein, 2008). At 9 months of age, infants react with more impatience when an adult is unwilling to give them a toy compared to when the person is unable to do so (Behne, Carpenter, Call, & Tomasello, 2005), and infants aged 12 months comprehend an adult’s informative pointing gesture to the location of a hidden toy (Behne, Liszkowski, Carpenter, & Tomasello, 2012). Moreover, already at 14 months of age, infants know what another person knows, in the sense of what the other person has and has not experienced in the immediate past (Moll and Tomasello, 2007), and they are able to represent another person’s visual perspective independently of their own, thus demonstrating Level-1 visual perspective taking abilities (Sodian, Thoermer, & Metz, 2007). Finally, infants as young as 6 and 9 months of age have been shown to reproduce a modelled action following a delay of up to 24 hr in tests using the deferred imitation paradigm (Jones & Herbert, 2006); 12-month-old infants demonstrated an understanding of others' intentions as rational choices in studies on rational imitation (Schwier, van Maanen, Carpenter, & Tomasello, 2006; Zmyj, Daum, & Aschersleben, 2009); and, 12-month-olds can use a nonverbal pointing gesture to make reference to absent entities (Liszkowski, Schäfer, Carpenter, & Tomasello, 2009). Interestingly, the ability to refer to absent entities (Bohn, Call, & Tomasello, 2015) and rational imitation (Buttelmann, Carpenter, Call, & Tomasello, 2007) have also been shown in studies with all great ape species and chimpanzees, respectively.

To summarize, animals other than great apes as well as human infants considerably younger than 18 months (i.e., the age at which mirror self-recognition typically starts to emerge) show impressive cognitive abilities in theory-of-mind tasks. Assuming that mirror self-recognition is a key indicator for animals and human children to progress to the level of noetic consciousness, these results indicate that the investigated cognitive abilities have evolved in animal species that possess anoetic consciousness (Table 1) and are mastered by human infants in early ontogeny when their level of consciousness is anoetic, too. Whether false-belief understanding requires cognitive abilities other than behavioral rules is addressed in the section "Implicit and explicit theory of mind abilities."

Self-awareness Associated with Mirror Self-recognition

In the literature, the ability of mirror self-recognition is considered to imply some form of self-awareness; however, it is disputed what type or level of self-awareness is involved. Schilhab (2004) distinguished between a "strong" and a "weak" interpretation of mirror self-recognition. She summarized that "according to the 'strong' interpretation, passing the mark test manifests advanced subjective self-awareness, while the 'weak' interpretation claims the capacity for visual-kinesthetic matching only" (p. 119) and concluded that scientific evidence is in favor of the "weak" interpretation. Similarly, Morin (2011, p. 370) stated that "all an organism requires to self-recognize is a mental representation of its own physical self; the organism matches the kinaesthetic representation of the body with the image seen in the mirror and infers that 'it's me'." However, at a closer look, the "weak" interpretation is not truly weak. To pass the mark test, a human infant must have a mental representation of its face (without the mark) and be able to compare this representation with the marked face reflected in the mirror (Bard et al., 2006). It is thus questionable, whether and which nonhuman animal species are able to do so. Recently, Gallup and Anderson (2018) reviewed current evidence from studies on mirror self-recognition and concluded that "despite claims to the contrary neither dogs, elephants, dolphins, magpies, horses, manta rays, squid, nor ants have shown compelling, reproducible evidence for self-recognition" (p. 16).

Amsterdam (1972) investigated the development of behavior shown by infants exposed to a mirror and found an age-related sequence of responses. From about 6 to 12 months of age, the reaction to the mirror image was that of a playmate, with a peak incidence at 6 to 8 months. Infants of this age group also observed their own image as they moved their bodies or a part of it, and the peak for such behavior was at 9 to 11 months. In the second year of life, avoidance behaviors (i.e., wariness and withdrawal) appeared, accompanied by self-admiring and embarrassed behavior starting at 14 months. Finally, from 20 to 24 months of age, the majority of the subjects demonstrated recognition of their mirror images. Likewise, both monkeys and chimpanzees initially responded to the mirror image as if they were confronted with an unfamiliar conspecific and directed social responses toward the reflection (Anderson & Gallup, 2011). In a developmental study, Lin et al. (1992) investigated the behavior of chimpanzees, aged 18 to 61 months, exposed to mirrors after being marked with children's make-up cream on the brow and forehead. They reported that all chimpanzees exhibited both contingent movements and self-directed responses to the body and face while looking at the mirrored image. Moreover, they found that individuals of the youngest age group (2-year-olds) displayed self-directed behavior but no self-recognition; they concluded that, similar to the observations made in human infants, contingent movements and self-directed behavior in front of a mirror developmentally precede mark-directed self-recognition in chimpanzees.

In addition to infants and great apes, elephants (Plotnik et al., 2006), dolphins (Morrison & Reiss, 2018) and magpies (Prior et al., 2008) were observed to test for behavioral contingencies when exposed to a mirror. Elephants showed repetitive, nonstereotypic trunk and body movements (both vertically and horizontally) in front of the mirror and rhythmic head movements in and out of mirror view; magpies moved repeatedly leftwards and rightwards or back and forth in front of the mirror; and dolphins displayed repetitive head and body movements in the vertical plane. Moreover, these animals were reported to produce mirror-guided self-directed behaviors. For example, elephants stuck their trunks into their mouths in front of the mirror, dolphins made movements allowing them to view body parts unobservable in the mirror's absence, and magpies touched the breast region outside the marked area in a mirror-mark test. Given the fact that, during ontogeny, human infants and chimpanzees perform contingent movements and self-directed behavior in front of a mirror before they are able to pass the mark test (Amsterdam, 1972; Lewis & Brooks-Gunn, 1979; Lin et al., 1992), it is questionable whether these behaviors can be taken as evidence for mirror self-recognition in nonhuman animals. Self-directed behavior and contingent movements could also be viewed as explorative behavior, without inferring possession of a self-concept. In line with this, Suddendorf and Butler (2013) argued that the visual self-recognition skills evident in humans and great apes indicate “a general capacity to collate representations” (p. 121), that is, a “more general ability to entertain and compare multiple mental models of the same thing” (p. 125). Similarly, Boyle (2017, p. 284) concluded that self-recognition “requires ‘objective self-awareness’ - the capacity for first person thought like ‘that’s me’.” Mirror self-recognition would thus require noetic consciousness, whereas both animals and infants can show contingent movements and mirror-guided self-directed behavior at the level of anoetic consciousness (Table 1). Exploring body parts as well as movements in front of a mirror also indicates that both human infants and animals with anoetic consciousness realize that primary representations of their body (e.g., sensory perception of self-touch, visual feedback when moving one's own limb) are markedly different from primary representations of other objects in the world (e.g., touching the skin of a conspecific, observing movements of a stone). Consequently, it is plausible to assume that they have a "body awareness" (Moore, Mealiea, Garon, & Povinelli, 2007; Morin, 2012) that includes awareness of the body as the center of action (i.e., an implicit "sense of agency"; David, Newen, & Vogeley, 2008; Morin, 2012).

Implicit and Explicit Theory of Mind Abilities

In standard verbal false-belief tests, different experimental paradigms have been used with children to assess their ability to recognize that the knowledge state of a person who did not witness an event they observed themselves may differ from their own knowledge state, implying that the person has a false belief. Examples of such paradigms are change-of-locations, unexpected contents, and unexpected-identity tasks (Wellman et al., 2001). As these tasks are typically verbal, they were carried out in children with adequate linguistic competence but not with pre-linguistic infants or nonhuman animals. In a meta-analysis, Milligan et al. (2007) found that children's language ability is significantly related to their false-belief understanding. Although the effect size for this relation was reduced in a second analysis including only studies that controlled for age, the authors assumed that age is not really an explanatory variable for false-belief understanding but rather a proxy for various maturational factors that may explain variation, an important one of which is language. Nevertheless, age is clearly related to children's performance in standard verbal false-belief tests. Typically, they do not pass these tests before the age of 4 years (Wellman et al., 2001).

In a study with 2- to 4.5-year-old children, however, Clements and Perner (1994) observed that, depending on age, subjects differed in their looking behavior when tested in a standard verbal false-belief test. Younger children up to 2 years and 10 months of age gave the wrong answer concerning the location of a hidden object in the false-belief condition and also erroneously looked at the wrong location (i.e., the object's real location). In contrast, 90% of the older children looked at the empty location, but only about 45% of the children in this age range gave that location as their explicit answer to the experimenter's question. The authors concluded that implicit false-belief understanding, indicated by the children's looking behavior, substantially precedes explicit understanding. More than 10 years later, several studies using violation-of-expectation paradigms confirmed that infants as young as 10 and 15 months show implicit false-belief understanding (Luo, 2011; Onishi & Baillargeon, 2005).

To account for the difference between children's explicit and implicit false-belief understanding, as evident in their verbal responses in standard false-belief tests and their anticipatory looking behavior in violation-of-expectation tasks, respectively, Apperly and Butterfill (2009) suggested that humans have two systems to track beliefs. They differentiated between an early-developing, cognitively efficient but inflexible capacity for tracking belief-like states and later-developing, more flexible but more cognitively demanding theory of mind abilities. In line with this view, Grosse Wiesmann et al. (2017) compared the performance of 3- and 4-year-olds in implicit and explicit false-belief tasks and found a significant developmental change. Both age groups passed implicit false-belief tasks, but 3-year-olds performed significantly below chance in explicit false-belief tasks. In addition, they reported that children’s performance in implicit and explicit false-belief tasks did not correlate. The authors thus concluded that “the processes underlying implicit false-belief tasks are different from later-developing explicit false-belief understanding” (p. 1). Also in support of the two-systems theory, Fizke, Butterfill, van de Loo, Reindl, and Rakoczy (2017) investigated 2- and 3-year-old children’s active helping behavior in a change-of-location false-belief task, concluding that their early theory-of-mind reasoning is possibly subject to signature limits as predicted by the two-systems account. Furthermore, Oktay-Gür and Rakoczy (2017) compared the development of performance in both false- and true-belief tasks in children aged 3 to 10 years and found that, in line with the predictions of performance limitations accounts, performance was negatively correlated between the two types of tasks and showed a U-shaped curve in true-belief tasks, such that 3- and 10-year-olds performed competently and the children between failed. Finally, Oktay-Gür, Schulz, and Rakoczy (2018) demonstrated that 2-year-olds performed competently only in implicit false-belief tasks that did not require an understanding of aspectuality (see Fizke et al., 2017; Rakoczy, 2017; Rakoczy, Bergfeld, Schwarz, & Fizke, 2015), also indicating signature limits in young children’s performance in implicit theory-of-mind tasks. In contrast, Scott and Baillargeon (2017) argued that processing difficulties, rather than limitations in false-belief understanding, account for young children’s failure at standard verbal false-belief tasks and stressed that 2.5- and 3-year-olds succeeded at traditional tasks with reduced processing demands (Rubio-Fernandez & Geurts, 2013; Setoh, Scott, & Baillargeon, 2016). Similarly, Scott, Richman, and Baillargeon (2015) questioned the minimalist account of early psychological reasoning. In a series of experiments with belief-inducing situations, they analyzed 17-month-olds’ looking behavior and found evidence indicating that infants in the second year of life can understand deceptive intentions to implant false beliefs in others. In the interpretation of their results, they suggested that these “are more consistent with a one-system view in which psychological reasoning is mentalistic from the start” (p. 51).

With nonhuman animals, experimental studies demonstrated that great apes showed false-belief understanding in an anticipatory looking test and an interactive helping task (Buttelmann et al., 2017; Krupenye et al., 2016), whereas rhesus monkeys failed to attribute a false belief to a human agent in violation-of-expectation tasks (Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Martin & Santos, 2014). As in studies with human infants (Burge, 2018), it is debatable whether false-belief understanding in great apes is based on implicit or explicit theory of mind abilities. In the discussion of their results, Krupenye et al. (2016) acknowledged that change-of-location false-belief tasks are open to an abstract behavior rule-based explanation, such that the apes could have solved “the task by relying on a rule that agents search for things where they last saw them” (p. 113), a behavioral rule suggested by Perner and Ruffman (2005). Regarding the apes’ performance in the helping task, the level of false-belief understanding necessary to be successful is not clear either. Buttelmann et al. (2009), using the same experimental paradigm with 18-month-old human infants, stated that it is an open question whether the infants’ false-belief understanding is of the same nature as that shown by 5-year-olds in standard verbal false-belief tasks. Thus, great apes may not need a concept of belief to determine how to help a person with a false belief (Andrews, 2018).

In a review on theory of mind abilities investigated in both developmental and comparative psychology, Butterfill and Apperly (2013) described the construction of a minimal theory of mind, suggesting that such a theory may enable those with limited cognitive resources, such as human infants and chimpanzees, to track others’ perceptions, knowledge states, and beliefs. In line with such thinking, Ruffman (2014) provided a framework outlining how children may develop an implicit understanding of behavior that allows success in certain theory-of-mind tasks before they develop an explicit understanding of mental states and argued that the latter is induced through maternal dialogue about mental states and the children’s own developing language and self-recognition skills. Accordingly, Rakoczy (2017) reviewed human developmental theory-of-mind research and concluded that children possess less sophisticated forms of tracking simpler mental states long before the explicit conceptual capacity to ascribe propositional attitudes emerges at around age 4. With regard to the three levels of consciousness outlined above, these patterns in human ontogeny and phylogeny would imply that implicit false-belief understanding is present in infants with anoetic consciousness and that great apes could also pass nonverbal false-belief tasks based on implicit false-belief understanding (Table 1). However, to explicitly understand false-belief states in others, autonoetic consciousness would be required. Interestingly, adult humans may nevertheless continue to engage in automatic analyses of others’ mental states (Schneider, Slaughter, & Dux, 2017), using a cognitive system possibly identical to the one already present in infants with anoetic consciousness (Edwards & Low, 2017).

Goal-directed Behavior and Episodic Future Planning

At the level of anoetic consciousness, nonhuman animals are able to store and update information about facts of the world based on procedural memory (Tulving, 1985). For example, both dogs and great apes showed signs of “surprise” in a violation-of-expectation paradigm when they found a food item in a container that did not correspond to the food item the experimenter had previously placed in that container (Bräuer & Call, 2011). Moreover, in a study using the information-seeking paradigm, great apes demonstrated that they are able to monitor their own memory and know that they could be wrong (Call, 2010). Similarly, orangutans and macaques learned to use an escape response, also called the uncertainty response, with which they could decline to complete difficult trials in spatial learning tests and discrimination tasks in animal metacognition studies (Smith, 2009; Suda-King, 2008).

Finally, episodic-like memory that allows (1) rats to retrieve a memory trace of a past experience in what-where-which tasks (Eacott & Easton, 2010), (2) pigeons to answer the unexpected question "where did you just peck?" (Singer & Zentall, 2007), and (3) implicit false-belief understanding shown by human infants (Onishi & Baillargeon, 2005) and great apes (Krupenye et al., 2016) in studies using violation-of-expectation looking time methods may be based on procedural memory abilities (Table 1). To summarize, lower-level mechanisms can be sufficient to explain metacognition (Crystal & Foote, 2009), mental time travel (Suddendorf & Corballis, 2007), and theory-of-mind (Apperly & Butterfill, 2009) abilities at the level of anoetic consciousness.

With regard to episodic future planning, the Bischof-Köhler hypothesis holds that animals other than humans are not capable of anticipating their future needs (Suddendorf & Corballis, 1997, 2007). In detail, the hypothesis suggests that nonhuman animals in a given motivational state (e.g., satiated after a meal) are not able to imagine a future motivational state (e.g., hunger after several days of unsuccessful foraging) that is different from their present state and, therefore, will not store food because they do not cognitively anticipate a future hunger state (Bischof, 1985, see passage on "mental time representation," pp. 540–543). The reason for this incapability is the lack of the concept of time as a continuum and the lack of a continuous self through time, concepts that are unique to humans and bound to autonoetic consciousness.

Not all planning for the future, however, goes beyond the present motivational state. Animals may well take actions to achieve a specific goal, typically situated in the near future, that satisfies the current motivational need. With animals at the level of anoetic consciousness, such actions may be based on innate or learned behavioral rules. To satisfy their hunger, for example, animals may use the odor of ripe fruits to find food (an association that can be innate) or return to a fruit tree on which they foraged the day before (based on learning). Thus, to investigate the ability for mental time travel in nonhuman animals, the experimental design must be such that both innate mechanisms and learning can be excluded as alternative explanations. The spoon test aims at meeting these conditions, in that the experimental animal ideally is given a single experience to form an association between the tool and the solution of a task (e.g., to use a hose to suck up a fruit soup). Moreover, in later test trials, the animal has to select the tool out of sight of the experimental apparatus (e.g., a container baited with fruit soup) and to keep it for a longer period before it has access to the apparatus. As mentioned above, great apes succeeded in such tests (Mulcahy & Call, 2006; Osvath & Osvath, 2008), whereas monkeys failed to do so (Bourjade et al., 2012; Paxton & Hampton, 2009), indicating that the apes' success could be due to mental time travel abilities.

With humans, Atance and Meltzoff (2006) found that children as old as 3 to 5 years tended to predict future food preferences in terms of their present motivational state and that their performance improved markedly with age. In a spoon test, 4- and 5-year-olds but not 3-year-olds were more likely to select a target toy in an experimental condition that involved its future use compared to a control condition assessing the simple preference for the toy (Suddendorf & Busby, 2005). Moreover, Scarf, Gross, Colombo, and Hayne (2013) reported that 4-year-olds were able to select the appropriate tool for future use when they were asked to do so following a delay of 24 hr or 1 week after initial task exposure, whereas 3-year-olds were only successful following a 15-min delay. Finally, Suddendorf, Nielsen, and von Gehlen (2011) found that 4-year-olds but not 3-year-olds performed above chance in two spoon tests with a 15-min delay between the presentation of the problem and the selection of a suitable object to solve it. These results suggest that children at the level of noetic consciousness face difficulties to pass the spoon test and that 4-year-olds with autonoetic consciousness "have acquired the basic cognitive components required to mentally construct specific future events" (Suddendorf & Redshaw, 2013, p. 135), that is, the ability for episodic future thinking (Table 1).

Critics stated that the positive results obtained in spoon tests with great apes should be taken with caution, as the experimental conditions cannot rule out alternative interpretations. With the study of Mulcahy and Call (2006), Scarf, Smith, and Stuart (2014) pointed out that the apes made their selections with the apparatus in view, raising the possibility that tool selection was cued. Furthermore, critics argued that the apes could have experienced a desire for the reward throughout the waiting period and that the experiment did not directly address the Bischof-Köhler hypothesis (Osvath & Martin-Ordas, 2014). Finally, the apes received a number of training trials, allowing for a simpler explanation in terms of reinforcement of the anticipatory act (Clayton, 2015). With the study of Osvath and Osvath (2008), Suddendorf, Corballis, and Collier-Baker (2009) proposed that one-trial associative learning of the apes, when sucking the fruit soup through the straw the first time, could explain that they continued to select this tool on each of the following trials. In his response, Osvath (2010) stressed that one-trial learning was pivotal to the experiment and an integral part of the design. Possibly, one-trial learning in such tasks is easier for great apes compared to other animals, as they are able to form secondary representations. Once they have made the association between the tool and the reward, the value of the tool is part of its secondary representation. This may also explain that, in Osvath and Osvath's (2008) study, the apes defended the tool over a period of 70 min while housed in a group before they gained access to the room containing the apparatus with the fruit soup. This interpretation matches Roberts and Feeney's (2009, p. 275) suggestion that the apes "could have chosen the hose because they knew its functional value for sucking up fruit soup without anticipating its use 70 min in the future." More generally, having noetic consciousness and being able, for example, to stick a representation of a hose into a representation of a rewarding apparatus, combining this with the representation of the self that sucks up the soup using the hose, may be the key for the understanding of insight learning (Shettleworth, 2012) observed in chimpanzees (Köhler, 1921). In addition, the ability to form secondary representations of goal states and goal-directed behaviors could explain route planning reported in studies with wild chimpanzees (Ban, Boesch, & Janmaat, 2014; Janmaat, Polansky, Ban, & Boesch, 2014; Normand, Ban, & Boesch, 2009) and orangutans (van Schaik, Damerius, & Isler, 2013). The performance of great apes in the spoon test and possibly of children younger than 4 years of age would thus be based on semantic memory and demonstrate the ability for semantic prospection

(Table 1) rather than episodic future thinking. They would use recalled information to anticipate a future situation without needing to project themselves into an episodically constructed future event (Osvath & Martin-Ordas, 2014). To conclude, the absence of an episodic cognitive system (autonoetic consciousness) does not preclude the ability to take actions for the future, and the capacity of the semantic cognitive system may be sufficient to produce and control goal-directed behavior in nonhuman animals (Raby & Clayton, 2009).

In line with this hypothesis, children younger than 4 years of age and at the level of noetic consciousness were shown to perform goal-directed behavior in experimental studies. For example, Bauer, Schwade, Wewerka, and Delaney (1999) provided 21- and 27-month-olds with the goal-state information (e.g., shook a rattle) before they gave them the disassembled component parts of the problem and encouraged them to produce the goal (e.g., said “now it's your turn, you make a rattle”). Children of both age groups showed evidence for planning and produced target actions to achieve the mentally represented goal. Similarly, Jennings (2004) presented children between the ages of 15 and 35 months with four types of mastery tasks that required representation of a goal and a chain of actions to complete the goal. She found that children in the youngest group (18 months old) typically paid little attention to goals and continued with the activity if they solved the task, whereas children in the oldest group (32 months old) typically met the specifically stated goal of the task and stopped their task actions when the goal was met. Episodic future thinking, characterizing autonoetic consciousness, may thus not be necessary to explain goal-oriented behavior in children less than 4 years of age.

What is Uniquely Human?

As elaborated in the previous sections, explicit false-belief understanding (Call & Tomasello, 2008; Penn & Povinelli, 2007) and the capacity for mental time travel (Suddendorf & Corballis, 2007; Tulving, 2005) are likely to be unique to human subjects, but great apes may have the capacity to entertain secondary representations (Whiten & Suddendorf, 2007). Consequently, autonoetic awareness is unique to the human species, but great apes may possess noetic consciousness. For individuals of other nonhuman animal species, anoetic consciousness is probably the adequate level to describe their awareness of their experiences. Taking up the hypotheses concerning milestones in the development of cognitive abilities proposed by Bischof-Köhler and Bischof (2007) and Suddendorf and Whiten (2001), the decisive points are whether the cognitive skills observed in nonhuman animals require the ability to become aware of frames of reference or can be explained by the ability to form secondary representations, respectively.

Current evidence also indicates that Level-2 perspective-taking abilities are linked to the level of autonoetic awareness (Table 1). In standard tasks for testing this capacity, children “have to confront two visual perspectives on the same object and understand that the same thing can be perceived in different ways” (Moll, Meltzoff, Merzsch, & Tomasello, 2013, p. 647), and it was found that they are able to do so at around 4 years of age. However, when the development of Level-2 perspective-taking was re-examined using a color filter technique, asking children how an object looked to an adult when she saw it through the filter, 36-month-olds were successful in solving the task (Moll & Meltzoff, 2011). To explain the age difference in the performance of the two tasks, Moll et al. (2013) concluded that 3-year-olds can take but not confront visual perspectives. In support of this interpretation, Surtees, Butterfill, and Apperly (2012) presented results suggesting that the Level-1/Level-2 distinction is based on two different cognitive processes. In contrast with findings from Level-1 perspective-taking, they found no evidence of automatic processing of Level-2 perspectives in 6- to 11-year-old children and human adults. Also consistent with the view that Level-2 perspective-taking abilities are bound to autonoetic consciousness, Karg, Schmelz, Call, and Tomasello (2016) reported that 6-year-old children but not chimpanzees engaged in Level-2 perspective-taking when they had to predict a conspecific's perspective that differed from their own.

As outlined in the section "Goal-directed behavior and episodic future planning," not all planning for the future has to rely on episodic prospection and autonoetic consciousness. Semantic future thinking at the level of noetic consciousness may explain goal-directed behavior observed in human children younger than 4 years of age and great apes. Likewise, young children's verbal communication about the past as well as episodic-like memory in great apes may be based on semantic rather than episodic memory abilities. Autobiographical memory develops relatively late and "it is not until the end of the preschool years that children come to have a subjective perspective on the past, which includes persistent internal states or stream of consciousness, that creates a continuous self through time" (Fivush, 2011, p. 572). However, children produce temporal terms such as "yesterday" or "last week" (Busby Grant & Suddendorf, 2011) and talk about the past much earlier. Fivush, Gray, and Fromhoff (1987) interviewed 29- to 35-month-old children about unique, distinctive events that they had experienced in the last 6 months. They found that the children recalled accurate information about such events; however, the amount of recall was not related to the age of the memory. To interpret these results, it is plausible to assume that, at the level of noetic consciousness, children are able to address secondary representations of past events and to retrieve them using semantic memory (Table 1). In line with this suggestion and in support of the hypothesis that great apes may have noetic consciousness, Martin-Ordas, Haun, Colmenares, and Call (2010, p. 333) stated that Panzee, the chimpanzee in Menzel's (1999) study, "may have updated her memory about spatial landmarks without recalling the food-hiding event."

It is still an open question as to how and when episodic memory skills emerge in human ontogeny. In a hide-and-seek task, 3-year-old children recalled less information than 4-year-olds when asked to verbally recall but showed an equivalent performance when asked to behaviorally show where the hiding event took place (Hayne & Imuta, 2011). The authors concluded that the results of their experiment illustrate age-related changes in episodic memory. However, the superior performance of 4-year-olds in the verbal recall test could also rely on their further developed semantic memory system. In support of their interpretation, Hayne and Imuta (2011, p. 321) reported that the children’s accounts of the hiding events “were described in the first person indicating that they had some recollection that the events had happened to ‘me’.” Correspondingly, Tustin and Hayne (2016) observed that 3-year-olds recalled a play situation with a train after both a 24-hr and a 1-year delay and recounted their past experiences of the train event from a first-person perspective. At the level of noetic consciousness, however, this first-person perspective could build upon the children’s ability to assign semantic memory contents to the secondary representation of the self. They would therefore have explicit memory of what happened to the “me” (Table 1) without episodic memory skills and autonoetic consciousness. In analogy, the ability to assign semantic memory contents to the “me” could also explain future-oriented talk in 3-year-olds (Hayne, Gross, McNamee, Fitzgibbon, & Tustin, 2011) without assuming that children are already capable of episodic foresight at this age.

Several studies with 3- to 5-year-old children found that the capacity to report about past and future events increased markedly with age (Busby & Suddendorf, 2005; Hayne et al., 2011; Suddendorf, 2010). This increase is possibly caused by the transition from noetic consciousness to autonoetic consciousness and the emergence of the episodic memory/prospection system in addition to the semantic system. Interestingly, these studies also revealed a significant positive correlation between children’s performance on yesterday and tomorrow questions, both regarding the quantity and the quality (i.e., answers that parents judged as correct) of responses. This result is consistent with the hypothesis that children’s memory of the past is related to their ability to think about the future (Martin-Ordas et al., 2014; Suddendorf, 2010), no matter whether the semantic or episodic system is involved. Evidence for the episodic/semantic distinction as well as the interplay between these two systems also comes from studies on memory and prospection in human adults with brain damage or neurodegenerative disorders. For example, Rosenbaum et al. (2005) reported the case of a man with large bilateral hippocampal lesions, who was incapable of recollecting any personal episodic incidents but had retained a great deal of semantic knowledge of the world, including knowledge about himself. Furthermore, De Luca et al. (2018) described a patient with retrograde amnesia following hypoxia, who was unable to imagine personal future events but could imagine fictitious events not self-relevant and not located in subjective time. Finally, Irish and Piguet (2013) reviewed the literature on studies assessing cognitive abilities of humans with neurodegenerative disorders and stressed the role of semantic memory for autobiographical retrieval of the past and simulation of future events.

Consciousness and Animal Welfare

Differences in cognitive abilities between animal species are important with regard to animal welfare. For example, an animal’s capacity to recall past events and to anticipate future events is crucial for the assessment of its welfare in a given situation (Lea, 2001). Assuming that great apes possess noetic consciousness, they are likely to have secondary representations of emotional experiences, such as anxiety, boredom, or feeling pain, and can link these to a secondary representation of the self. Consequently, they could explicitly “know” about painful events that happened to the “me” in the past based on semantic memory. However, as great apes (and other nonhuman animals) lack autonoetic consciousness, they are not able to mentally travel back in time and remember episodes associated with painful experiences. Of course, past experiences are not only significant for the well-being of great apes but also for animals with anoetic consciousness. Implicit memories of events that elicited negative and positive emotions in past situations can induce anticipatory joy or fear in the present by virtue of learning of associations between cues and emotional events (Mendl & Paul, 2008). Based on procedural memory, for example, dogs get excited when the owner seizes the leash to go for a walk, and cats try to escape the veterinarian who gave them an injection 3 months ago.

Referring to the distinction made by Block (1995) between *phenomenal consciousness* (the ability to have primary representations of, for example, visual stimuli or painful stimulation) and *access consciousness* (the ability to think and reason [i.e., to form secondary representations]), Dawkins (2015) pointed out that the science of animal sentience is about phenomenal consciousness. Although primary representations are of a private nature and, therefore, not directly accessible to science, most people are convinced that animals feel pain when injured and suffer from inappropriate housing, even those with anoetic consciousness. Animal welfare science takes up this concern and aims at developing housing conditions and management procedures that are adapted to the animals’ behavioral organization (Wechsler, 1995, 2007; Wechsler & Lea, 2007). However, while this approach is sufficient to meet the motivational needs of animals with anoetic consciousness, specific studies are necessary with great apes to identify additional needs possibly arising from noetic consciousness.

With regard to animal welfare, it is also of interest whether or not nonhuman animals experience negative emotional states themselves when they see or hear a conspecific stressed or exposed to a painful procedure, such as surgical castration or dehorning. However, with different animal species and depending on their level of consciousness, different mechanisms could be responsible for such effects, ranging from emotional contagion to cognitive empathy (see Preston & de Waal, 2002, for a review). Whereas emotional contagion is a phylogenetically old mechanism that does not require self–other differentiation (Bischof-Köhler, 2012), cognitive empathy is characterized by an understanding of what caused the conspecific’s emotional state (de Waal, 2008) and is possibly limited to subjects possessing an explicit theory of mind. Consequently, emotional contagion is already present at the level of anoetic consciousness in nonhuman animals, whereas cognitive empathy could be linked to autonoetic consciousness typical of humans older than 4 years of age. Again, great apes may attain an intermediate stage because they might have the capacity to entertain a secondary representation of the “you” (Table 1). In line with this assumption, Koski and Sterck (2010) described an intermediate cognitive level of empathy (“veridical empathy”), reached by human children by the end of the second year, and hypothesized that “chimpanzee empathy exceeds direct, unregulated emotional contagion of young infants, but does not reach the level of cognitive empathy of a 4-year-old human” (p. 51). To conclude, animals possessing anoetic consciousness are likely to interpret signs of stress and pain in a conspecific directly as threatening to themselves, whereas great apes, in addition, may understand that another's situation can be different from one's own. Moreover, noetic consciousness may enable nonhuman animals to have empathic concern for a conspecific being harmed that goes beyond emotional compassion.

Finally, the three levels of consciousness outlined in this review probably have a major impact on how both positive and negative emotional states are experienced by nonhuman animals. An adult human being experiences emotions as subjective states, embedded in the self and open to introspection. In contrast, animals not possessing autonoetic consciousness do not have an introspective self and, at the level of anoetic consciousness, also lack a secondary representation of the "me" to which emotional states could be tied. Thus, the question arises: Who is suffering and feeling pain when there is no introspective subject in the case of anoetic or noetic consciousness? Whatever the answer, it is plausible to assume that the experience of emotional states is fundamentally different in animals not possessing autonoetic consciousness. However, these philosophical considerations should not stop us from taking action, preventing pain in animals, and adapting the housing conditions to their behavioral needs. Irrespective of the level of consciousness, animals clearly indicate that they seek and avoid situations associated with positive and negative emotional states, respectively; moreover, we readily attribute such states to young human children possessing anoetic or noetic consciousness.

Concluding Remarks

The main conclusions of this review are in support of lower-level explanations of cognitive abilities investigated in both animals and human children. Autonoetic consciousness and the associated cognitive abilities, an explicit theory of mind and a continuous self through time, are unique to humans. Taking temporal and spatial patterns of stimuli into account, nonhuman animals and pre-linguistic infants may use behavioral rules in theory-of-mind tasks. Concerning mental time travel abilities, the semantic cognitive system may be sufficient to produce the goal-directed behavior observed in nonhuman animals and children younger than 4 years of age. However, research into the cognitive abilities of animals is a "work in progress." Over the last years, remarkable results have been obtained in experimental studies addressing theory of mind and mental time travel abilities in nonhuman animals. Many of these studies were done with primates, especially with great apes. Therefore, future research covering a wider range of animal species may add important information to the picture outlined in the present review.

In my view, several research topics are of special interest with regard to the three levels of consciousness. The results of most studies on mirror self-recognition in animals other than great apes are based on experiments with very few individuals. To accurately distinguish between anoetic and noetic consciousness, mirror-mark tests should be replicated with larger sample sizes and with a larger variety of animal species. Moreover, mark-directed behavior should be differentiated clearly from accidental touching (or otherwise inspecting) the face or parts of the body unobservable in the mirror’s absence. Similarly, it would be interesting to do more studies using violation-of-expectation tasks with animals other than nonhuman primates to explore their mindreading abilities. As infants younger than 18 months of age may solve this kind of false-belief tasks using behavioral rules, it could be that animals, at the level of anoetic consciousness, also apply such rules. Furthermore, to differentiate between anoetic and noetic consciousness, experimental studies exploring the ability of insight learning in nonhuman animals could be of importance. Again, such studies should be carried out with an appropriate sample size and a detailed analysis of the animals’ behavior, ruling out lower-level explanations of successful performance. With regard to episodic future thinking, experimental designs similar to that of the spoon test (i.e., ones in which subjects have to take action for future events) but not involving tool use should be developed to rule out the possibility that the study animals save a tool for future use because they know of its functional value. Finally, additional studies investigating whether nonhuman animals have Level-2 perspective-taking abilities could shed light on the transition from noetic consciousness to autonoetic consciousness.

Having emphasized the importance of lower-level behavioral mechanisms explaining animals’ and human children’s performance in studies on theory of mind and episodic-like memory, I would like to mention that these mechanisms are, though amazing, within the range of behavioral rules identified in studies on behavioral ecology. Hence, those in favor of more sophisticated cognitive processes may underestimate the capability of a vertebrate brain, shaped by natural selection over millions of years and equipped with both innate behavioral rules and predispositions “to learn about and act on the perceptual relations between events, properties, and objects in the world” (Penn, Holyoak, & Povinelli, 2008, p. 110).

After searching the literature on cognitive abilities of children at the level of noetic consciousness, I also conclude that the capability of the semantic memory system is probably underestimated. Linking the secondary representation of the self to secondary representations of past events and goal-states enables children to report past events in the absence of episodic memory and to plan goal-directed behavior in the absence of episodic foresight. Moreover, secondary representations may be the key to explaining behaviors based on semantic memory as well as semantic future planning abilities observed in great apes.

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