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Review

Body and self in dolphins

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ABSTRACT

In keeping with recent views of consciousness of self as represented in the body in action, empirical studies are reviewed that demonstrate a bottlenose dolphin's (*Tursiops truncatus*) conscious awareness of its own body and body parts, implying a representational “body image” system. Additional work reviewed demonstrates an advanced capability of dolphins for motor imitation of self-produced behaviors and of behaviors of others, including imitation of human actions, supporting hypotheses that dolphins have a sense of agency and ownership of their actions and may implicitly attribute those levels of self-awareness to others. Possibly, a mirror-neuron system, or its functional equivalent to that described in monkeys and humans, may mediate both self-awareness and awareness of others.

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Contents

1. Introduction	527
2. Brief overview of bottlenose dolphin society	527
3. The lure of the dolphin brain	527
4. Animal consciousness	529
5. Some neurological underpinnings for consciousness	530
6. Animal self-awareness	530
7. Body and self	531
8. Body Image and body schema	532
9. Does the dolphin have a body image?	532
10. Agency and ownership of actions and the body as a basis for consciousness of self	534
11. Evidence for the senses of agency and ownership in dolphins: “self-imitation” studies	535
12. Mirror neuron system: distinguishing self and other, and facilitating social imitation	537
13. Social imitation by dolphins as evidence for consciousness of self and other	538
14. Conclusions	539
Acknowledgments	541
Appendix A. Supplementary material	541
References	541

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1. Introduction

What does a dolphin understand about its own body and self?

Asking this about a dolphin, in particular the well-studied *bottlenose* dolphin (*Tursiops truncatus*), is timely not only because of emerging neurological and behavioral interest in “the embodied agent” (de Vignemont, 2011; Tsakiris & Haggard, 2005) and in brain mechanisms that modulate the representation of the body in the brain (Arzy, Thut, Mohr, Michel, & Blanke, 2006; Berlucchi & Aglioti, 1997; de Vignemont, 2011; Farrer & Frith, 2002), but because many studies of this dolphin species have revealed the remarkable development of its brain and its extensive repertoire of behavioral, cognitive, and social skills. Many of these skills are convergent with those reported for chimpanzees (Herman, 1980; Marino, 2002), allowing for analyses of common structures and processes that may stretch across the seemingly impassable evolutionary and, ecological boundaries separating these two species.

I begin with a brief overview of bottlenose dolphin society to illustrate its complexity and follow this with a summary of some recent findings on the brain of this species. I then summarize some concepts of animal consciousness, selfhood, and self-awareness, especially body awareness, as well as noting some proposed neurological underpinnings from human consciousness studies that might be used to index conscious states in animals. I review mirror self-recognition findings that are suggestive of self-awareness in some animal species, including dolphins, and note that parsimony may in some cases demand higher-level interpretations of animal behaviors, as has been proposed for the findings on animal metacognition. In each of the next several sections, I first pose a question about some aspect of body awareness and then provide data from dolphin studies that bear on that topic. The aspects include body image and schema, agency and ownership, and self- and social-imitation and their possible relation to mirror neurons or mirror systems. Finally, I conclude with an assessment of how these various findings bear on the original question posed.

2. Brief overview of bottlenose dolphin society

The bottlenose dolphin is one of about 67 species of cetaceans, a diverse group divided into two suborders, the toothed whales (odontocetes, ca. 73 species) and the baleen whales (mysticetes, ca. 14 species) (Committee on Taxonomy, 2009). As a group, the cetaceans are highly successful ecologically having invaded every oceanic niche from the polar regions to the tropics, as well as colonizing some of the freshwater river systems of South America, India, Pakistan, and China. The natural history of a few of these species, the humpback whale, sperm whale, killer whale, and bottlenose dolphin, has been revealed through extensive, long-term field studies. Findings for the bottlenosed dolphin, a species (together with sister species) found worldwide in temperate and tropical waters, are that its societies vary somewhat in structure with the ecology of the region but are characterized by complex associations between individuals, some enduring and some transient (Connor, Wells, Mann, & Read, 2000; Wells, 2003). Vocalizations are the principal means of communication (Herman & Tavolga, 1980) but vision is also well developed and serves many of the species' behavioral and social functions (Madsen & Herman, 1980).

The intricacy and complexity of bottlenosed dolphin society has been revealed most intimately in a population inhabiting Shark Bay in western Australia. Individuals in that society may maintain as many as 100 different social relationships (Connor, 2010). Males form stable alliances in pairs or trios (first-order alliances) that can last for years; members of an alliance collaborate to capture and control individual females. Second-order alliances may form between first-order alliances to take away a female from another alliance or to defend against others seeking to capture their females (Connor, 2007; Connor, Smolker, & Richards, 1992). Additionally, some second-order alliances may associate with additional males to form third-order alliances, extending the network of associations and allowing for a wider resource of cooperating males for taking females or defending against others (Connor, 2007, 2010; Connor & Mann, 2006; Connor, Watson-Capps, Sherwin, & Krützen, 2010). According to Connor et al. (2010, p. 4), “Only humans and Shark Bay bottlenose dolphins are known to have multiple-level male alliances within a social network. It is unlikely a coincidence that humans and dolphins also have in common the largest brains, relative to body size, among mammals.”

3. The lure of the dolphin brain

The brain of the bottlenosed dolphin (and of several other species in the dolphin family—the delphinidae) is exceptional in its size and development (Hof, Chanis, & Marino, 2005; Morgane, Jacobs, & Galaburda, 1986; Oelschlager & Oelschlager, 2009; Ridgway, 1986a, 1986b), and is exceeded only by the human in the ratio of brain weight to body weight, the so-called “Encephalization Quotient” (EQ) (Jerison, 1973). Although not without its detractors as a comparator of relative brain size (e.g., Byrne, 1996; Connor, 2007; Holloway, 1974; Manger, 2006), EQ measures the degree of departure of the observed brain weight of a particular mammalian species from its expected brain weight based on the regression of brain weight on body weight for a large sampling of mammalian species. EQs greater than 1.0 index a degree of encephalization greater than expected. EQs for humans of about 7.0 are the highest measured, while EQs for five species in the dolphin family, including the bottlenosed dolphin, range from 4.14 to 4.95, significantly exceeding EQs for the anthropoid apes and for all of the remaining cetacean species measured (Hof et al., 2005; Marino, 1998, 2009; Ridgway, 1986b). Further, the cerebral cortex of the bottlenose dolphin brain (and of other odontocete brains) has greater and more complicated surface foldings (convolutions or

gyrification) than the human brain (as well as exceeding all other noncetacean animals in that dimension), and hence has greater relative surface area, although its reduced cortical depth results in a total cortical volume relative to the total brain less than that of the human (Ridgway, 1986a, 1986b, 1990). Given these and other distinctive and intriguing characteristics of the dolphin brain it is understandable that its function and characteristics have long been of interest, ranging from naked speculation and conjecture about extant languages (e.g., Lilly, 1961, 1967), to empirical study and mapping of cognitive skills in laboratory settings (e.g., Herman, Richards, & Wolz, 1984; Kellogg & Rice, 1964; Kilian, Yaman, Von Fersen, & Gunturkun, 2003; Smith et al., 1995; Xitco, Gory, & Kuczaj, 2001; also see reviews in Herman, 1980, 1986, 1987, 2002, 2006), to detailed anatomical and physiological study (e.g., Breathnach, 1960; Hof et al., 2005; Marino et al., 2001; Morgane et al., 1986; Oelschlagel & Oelschlagel, 2009; Ridgway, 1990). The behavioral studies of captive bottlenose dolphins have revealed extensive cognitive skills consonant with the complexity of the brain. Many of these skills are convergent with those demonstrated in the anthropoid apes (Herman, 1980, 1987; Marino, 2002; Marino et al., 2007). The noted intricacies and complexities of the bottlenose dolphin society in Shark Bay in western Australia underscore the potential utility of advanced cognitive skills for navigating through that extensive social matrix.

There has been conjecture as to the evolutionary pressures that might have selected for the large size of the dolphin brain, including that it results primarily from the value of passive listening and echolocation in an underwater world of limited visibility, yielding the observed hypertrophy of the auditory areas (e.g., Oelschlagel, 2008; Ridgway, 1986a). However, this argument must contend with several notable exceptions. For example, the insectivorous bats, the group of bats feeding on flying insects and having the most sophisticated echolocation system among all bats, have small brains and low EQs. Examination of the brain and body weights of 20 species of insectivorous bats listed by Hutcheon, Kirsch, and Garland (2002) reveals that all 20 have EQs falling below 1.0, meaning that brain sizes are smaller than expected given the corresponding body sizes. These bats do have relatively larger auditory processing areas (cochlear nuclei complex and superior olivary complex) than do fruit eating and nectar sipping bats, which do echolocate but rely more on vision and olfaction, suggesting that echolocation and attendant auditory capabilities can be supported through specialized areas without overall enlargement of the brain or extensive enlargement of the cerebral cortex. As another example, the harbor porpoise with a brain weight and body weight each less than a third that of the bottlenose dolphin (Marino, 1998) has an echolocation system that may be comparably sophisticated (e.g., Kastelein, Schooneman, Au, Verboom, & Vaughan, 1997). An additional problem for the auditory hypothesis of brain enlargement is that in many circumstances dolphins may use vision preferentially to echolocation (Herman, 1990, 1991). Visual resolution capability is good both underwater and in air (Herman, Peacock, Yunker, & Madsen, 1975) and is adapted for both bright light and dim light (through special pupillary adjustments and an extensive tapetum acting to amplify received light) (Madsen & Herman, 1980). Actually, the auditory and visual senses seem closely integrated. The auditory and visual primary cortical areas adjoin each other, unlike their spatial separation in humans and other terrestrial mammals (Morgane et al., 1986, Fig. 5.2). The proximity of these areas may underlie the ability of the dolphin for cross-modal recognition of objects across the senses of vision and echolocation, suggesting that echolocation, like vision, yields a representation (“image”) of the shape of the target object (Herman, Pack, & Hoffmann-Kuhnt, 1998; Pack, Herman, Hoffmann-Kuhnt, & Branstetter, 2002).

The so-called thermogenic hypothesis of brain enlargement in dolphins (Manger, 2006) contended that enlargement was simply a response to the cooling of oceanic waters during the Eocene–Oligocene transition (when odontocetes began to emerge from the ancestral Archaeoceti), leading to a consequent great increase in the number of glial cells to control brain temperature through metabolism of glycogen (glycogenolysis). To support his hypothesis, Manger asserted that there was no convincing evidence for cognitive complexity in dolphins. Manger’s arguments were reviewed by a large group of experts in brain anatomy and physiology, paleontology, and marine mammal field and laboratory behavioral and cognitive studies, and deemed flawed or misinformed in its key assertions (Marino et al., 2007, 2008; also see Marino, McShea, & Uhen, 2004).

The most compelling arguments for the evolution of the large size and complexity of the dolphin brain are those that invoke social pressures, as first suggested by Herman (1980) and buttressed by studies and observations reported, for example, in Connor (2007), Marino et al. (2007), and Herman (2006). The social intelligence hypothesis was advanced earlier by Jolly (1966) for the evolution of intelligence in primates, developed further by Humphrey (1976), and illustrated at length through field and laboratory studies of social behaviors (mainly in primates) in such works as Byrne and Whiten (1988) and in the various chapters in the compendiums of Whiten and Byrne (1997) and de Waal and Tyack (2005). Simply stated, effective integration into a society that favors both collaboration and competition with peers, emphasizes the recognition of numerous individuals and their encounter histories and propensities, and is structured in several of its components as nested alliances (alliances within alliances), as characterizes bottlenose dolphin society in Shark Bay, Australia (Connor, 2007, 2010; Connor & Mann, 2006; Connor et al., 1992, 2000) and also human societies, places a premium on social intelligence and the consequent benefits of navigating successfully through a complex social structure. In support of this social hypothesis, it is interesting that some recent work has revealed the presence of von Economo neurons in the neocortex of bottlenose dolphins and in several other odontocete cetaceans (Butti, Sherwood, Hakeem, Allman, & Hof, 2009). These neurons, originally thought to occur only in humans and great apes and to be part of the circuitry supporting human social networks (Allman, Watson, Tetreault, & Hakeem, 2005), have now been found in elephants and in several of the great whales, as well as in the odontocete cetaceans, including the bottlenose dolphin. According to Butti et al. (2009, p. 254) these neurons are believed to “represent a possible obligatory neuronal adaptation in very large brains, permitting fast information processing and transfer... in relation to emerging social behaviors.”

4. Animal consciousness

The scientific study of animal consciousness has flourished in recent years through a reawakening of the topic as a proper venue for science (Baars, 2005; Burghardt, 1985; Burghardt & Bekoff, 2009; Cartmill, 2000; Griffin, 1976, 1981, 1984, 2001; Humphrey, 1983). The early 20th century banishment of consciousness and other mental experiences from mainstream psychology and biology, especially for animals (Bekoff & Allen, 1997; Greenspan & Baars, 2005), was traced by Rollin (1990) to the emergence of new reductionist values championing empiricism and eschewing subjective (unobservable) phenomena, as promulgated in philosophy by the logical positivists (see Richardson, 2003; Richardson & Uebel, 2007), in psychology by the behaviorists (Skinner, 1938; Watson, 1913), and in biology by the early classical ethologists. Tinbergen (1951), for example, stated, “The ethologist does not want to deny the possible existence of subjective phenomena in animals, he claims it is futile to present them as causes, since they cannot be observed by scientific methods” (p. 5).

The “cognitive revolution” that later swept over psychology and related fields beginning in the late 1950s and early 1960s (Baars, 1986; Miller, 2003) was in part a response to these reductionist strictures but was also influenced by new information-processing concepts that provided models for the throughput (the mental events, constructs, and processes) from stimuli to responses (e.g., Broadbent, 1958; Lindsay & Norman, 1977; Miller, 1956). Faw (2009) described the subsequent growth of consciousness science as occurring in two stages, from 1980 to 1994 (a transition from the *pre-paradigmatic* stage to the *normal science* stage, Kuhn, 1962), and from 1994 to the present as the early stage of normal consciousness science.

The last quarter or so of the 20th century in fact witnessed many seminal studies of animal cognition and consciousness that began to reveal much of the range, character, and distribution of animal mental capabilities and processes. Noteworthy among these were Gallup’s study of mirror self-recognition in chimpanzees as an indicator of self-awareness (Gallup, 1970); Savage-Rumbaugh’s studies of chimpanzee and bonobo capabilities for sign language comprehension and production (Savage-Rumbaugh, 1986; Savage-Rumbaugh et al., 1993); Herman’s studies of dolphin capability for comprehending artificial gestural or acoustic languages (Herman et al., 1984); Premack and Woodruff’s (1978) innovative study of the “theory of mind” in a chimpanzee (see also Byrne & Whiten, 1988 for considerations of Machiavellian intelligence in primates); the discovery of semantic communication in wild vervet monkeys (Seyfarth, Cheney, & Marler, 1980); the finding of multiple levels of alliances in male bottlenosed dolphins (Connor et al., 1992); the demonstration of metacognitive abilities in a dolphin (Smith et al., 1995) and in monkeys (Cowey & Stoerig, 1995); and findings of episodic-like memory in scrub jays (Clayton & Dickinson, 1998).

Griffin’s books (Griffin, 1976, 1981, 1984, 1992, 2001) were particularly influential in challenging comparative psychologists and ethologists to take up the study of animal awareness, thinking, and consciousness. Griffin proposed a new field of study, cognitive ethology, which would extend the investigation of animal cognition and consciousness beyond the laboratory into the animal’s natural world (for reviews of Griffin’s books and his contributions to “seeding” the study of animal consciousness, see Baars, 2005; Burghardt, 1985; Gross, 2005; Ristau, 1991; Speck, 2005). Griffin’s review of field studies and observations of animal behavior and societies (Griffin, 2001) suggested to him that in the least animals should be credited with perceptual consciousness but perhaps not with reflective consciousness, which may be uniquely human (also see Shettleworth, 1998). However, recent findings on animal metacognition that reveal an animal’s ability to access the state or content of its perceptions, memories, or knowledge (Foote & Crystal, 2007; Fujita, 2009; Hampton, 2001; Smith, Shields, & Washburn, 2003; Smith et al., 1995) might be interpreted as indexing a form of reflective consciousness. Reductionist attempts to explain metacognition through associative learning (e.g., Carruthers, 2007; Jozefowicz, Staddon, & Cerutti, 2009) were challenged by Smith and colleagues (Smith, 2009; Smith, Beran, Couchman, Coutinho, & Boomer, 2009) who argued that much of the metacognition data cannot be accommodated by lower-level interpretations. Instead, the close isomorphism between human and animal uncertainty responses, in which a subject may choose to opt out of a difficult discrimination or memory test, suggests common functional mechanisms. Browne (2004), noting the similarity of animal and human strategies when experiencing uncertainty in metacognition tasks, stated, “It is parsimonious to explain close similarities in complex behavior patterns, both within and especially between species, by invoking the same kind of psychological mechanism (p. 642).” Smith (2009) argued that imputing conscious awareness to (some) animals in metacognition tasks is more parsimonious than low-level descriptions as “it explains many positive and negative results directly” (p. 395). Shea and Heyes (2010) suggested that good evidence for animal consciousness would be the transfer of successful performance on one metacognitive task to other metacognitive tasks. Smith (2009) in fact cites two studies (Fujita, 2009; Hampton, 2001) demonstrating just that, successful transfer of an uncertain response to novel (untrained) test situations. Also, Kornell, Son, and Terrace (2007) showed that Rhesus macaques successfully transferred a post-test confidence judgment of the correctness of their response on a perceptual task to new perceptual tasks and to a novel memory task. Transfer tests are powerful tools for clarifying that an animal has learned a concept and not just an S-R association (see e.g., transfer examples in Herman, Pack, & Wood, 1994; Herman, Uyeyama, & Pack, 2008).

In general, the liberation of “consciousness” from its early 20th century fetters has been welcomed by many contemporary researchers into animal (and human) behavior, and its resurrection is dramatically illustrated by the statistic presented in Baars (2005): “Today, some 5000 articles per year cite the term ‘consciousness’ in the scientific literature” (p. 12).

5. Some neurological underpinnings for consciousness

Animal consciousness may sometimes be inferred from behavioral responses that seem dependent on or “something like” a state of conscious awareness as experienced in humans. The metacognition studies are an example of this type of inference as are, arguably, the studies of mirror self-recognition in chimpanzees (Gallup, 1970) and the demonstration of episodic memory in scrub jays (reviewed in Clayton, Griffiths, Emery, & Dickinson, 2001; cf. Tulving, 1983). Alternatively, consciousness might be implied through homologies of neural processes of animals with those of humans engaged in tasks involving conscious awareness. Thus, Seth, Baars, and Edelman (2005) describe three well-established brain indices of humans consciousness that might be used to infer consciousness in animals: the EEG “consciousness signature” of irregular low amplitude, fast electrical activity; activation of the thalamocortical complex; and widespread brain activity as contrasted with local cortical activity. Similarly, Edelman and Seth (2009) propose using the correlation of human accurate report and observed neural responses as a benchmark for assessing evidence from studies correlating animal behavior and corresponding neural activity. Northoff and Panksepp (2008) suggest that humans and animals share a “core self” through “homologous neural networks in the subcortical–cortical midline system that provide a primal form of self-representation across mammalian species (p. 259).” According to these authors, the core self emerged early in mammalian evolution to facilitate the fundamental living skills of reproduction and survival. Similarly, Baars (2005) summarized neurological evidence suggesting “consciousness is a basic biological adaptation, with an evolutionary basis like any other (adaptation) (p. 10).” These references to homologous mental structures and processes for self-cognizance in humans and other animals are in keeping with Darwin’s (1871) stance that the difference in mind between humans and the higher animals, while certainly great, is one of degree and not of kind, a stance re-emphasized by Griffin in the sub-title of his 1976/1981 book: *Animal Awareness: Evolutionary Continuity of Mental Experience*.

Early mirror neuron studies showed that for macaque monkeys self-initiated transitive actions and observation of those same actions by others activated the same mirror-neurons in the pre-motor cortex, possibly allowing for interpretations or predictions of the actions of others based on one’s own stored motor representations (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Similar findings were observed for humans, although human studies were based on brain imaging recordings (e.g., fMRI, PET) and thus lacked the single-neuron resolution attained in the monkey studies; therefore, the activated areas were referred to as the mirror neuron system (e.g., Buccino et al., 2001; Oztop, Kewato, & Arbib, 2006). These initial studies were followed by a wave of new studies exploring and extending the findings on mirror-neuron systems into such areas as facial expressions, emotions, intransitive actions, sense of self and other, imitation, social intelligence, and even action words in language (e.g., Arbib, 2002; Buccino et al., 2004; Gallese, 2007, 2008; Jirak, Menz, Buccino, Borghi, & Binkofski, 2010; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001; Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006; Sinigaglia & Rizzolatti, 2011). Until recently, it could be claimed that there was no substantial evidence for mirror neurons in humans akin to those discovered in monkeys, as the single-cell recordings obtained from monkeys were not available from humans (e.g., Lingnau, Gesierich, & Caramazza, 2009). However, a recent study by Mukamel, Ekstrom, Kaplan, Iacoboni, and Fried (2010) did obtain single-cell recordings from 21 patients undergoing surgical removal of epileptogenic brain regions; these patients had volunteered to allow single cell recordings and to participate in viewing filmed images of facial expressions and movements of people as well as executing various movements themselves. The results showed activation of some of these single neurons on performing an action and on seeing it performed by another, as was found earlier in monkeys, but there was no similar level of activation on observing or executing various facial expressions. Thus, visual information, of itself, was not sufficient to evoke the responses obtained. The brain regions available to Mukamel et al. were not the same as those recorded in monkeys, but the authors viewed this as demonstrating that mirror neurons, though only a small minority of neurons in any observed area, may exist in many brain regions and not just the pre-motor cortex, as has been noted also in the review by Sinigaglia and Rizzolatti (2011). Consistent with this interpretation, Oztop et al. (2006), remarking that the imitation and language functions allegedly subserved by mirror neurons or mirror systems are not within the capabilities of macaque monkeys, argued that in humans these functions may “instead depend on the embedding of (mirror-neuron) circuitry homologous to that of the macaque in more extended systems within the human brain” (p. 255). More research to document the occurrence and function of mirror neurons in humans is certainly warranted.

6. Animal self-awareness

Burghardt and Bekoff (2009) noted that “almost all scholars recognize the existence of various kinds and levels of consciousness (p. 40).” Yet, most of the scientific study of animal consciousness (as well as consciousness in infants and young children) has focused primarily on self-consciousness rather than on consciousness *per se* (Faw, 2009). Self-consciousness, like consciousness itself, may come in many kinds and levels. For example, Legrand (2007a) distinguishes between self-consciousness in which the self is the subject (“I”), and self-consciousness in which the self is the object (“me”). The most studied type of self-consciousness in animals has been self-awareness as indexed through mirror self-recognition (MSR), first demonstrated in chimpanzees by Gallup (1970). Gallup applied a red odorless dye to the head and ear of anesthetized chimpanzees that had previous mirror experience. After recovery and with the mirror again available Gallup observed that some chimps reached for the marks on their own heads on observing their mirror image. For Legrand (2007a), the perceiving

chimpanzee would be the self as subject while the perceived image would be the self as object. Following on Gallup's initial findings, there has been wide application of the MSR technique to different animal species as investigators ostensibly search for the phylogenetic range of self-awareness and its associated functions or links. The technique has also been applied to infants and young children to determine the developmental stage at which MSR emerges (at about 18–24 months, Amsterdam, 1972; Johnson, 1983). Understandably, there has been widespread discussion, pro and con, of MSR in the literature (e.g., see many of the chapters in Parker, Mitchell, & Boccia, 1994).

Gallup's (1970) procedures thus provided an innovative method for investigating self-awareness experimentally, and for a time MSR served as the *sine qua non* for revealing self-awareness in animals behaviorally. Passing the mirror test, according to Gallup, implies that the individual has a *concept* of self. Gallup acknowledged, however, "there is much more to being self-aware than merely recognizing yourself in a mirror" (Gallup, 1994, p. 48). Similarly, Legrand (2007b) remarked, "self-consciousness comes in many forms and degrees and does not only emerge the moment one recognizes one's own mirror image (p. 584)." Similarly, Mitchell (1994) lamented, "Given the many different senses of self in human beings, it is unfortunate that the research on self in nonhuman animals has become so focused on the study of MSR (p. 84)." He then stressed the need to examine forms of self unrelated to MSR. Gallup (1977) in fact acknowledged this broader view, stating that MSR is simply an affirmation of a pre-existing concept of self. That MSR in human infants only fully appears in the second year of life (Johnson, 1983) suggests that the self-concept is an emergent property of the child's expanding social experiences (Gallup, 1977; Lewis, 2011; Mead, 1934).

The presence of MSR in the great apes (with the possible exception of the gorilla (but see Patterson & Cohen, 1994; Posada & Colell, 2007) and not in the lesser apes or monkeys (Gallup, Anderson, & Shillito, 2001; Platek & Levin, 2004; Suddendorf & Collier-Baker, 2009) was seen by some as an evolutionary pointer to the development of consciousness in humans. Earlier claims that only the great apes and humans (Hominoidea) were self-aware (Povinelli & Prince, 1998), based on the MSR test, have been discounted by findings of mirror self-recognition in dolphins (Reiss & Marino, 2001) and elephants (Plotnick, de Waal, & Reiss, 2006) among various mammals tested. That great apes, dolphins, and elephants are all large-brained, highly social animals suggests that mirror self-recognition, or self-awareness in general, may be an emergent property of a more general cognitive capacity functioning within an extensive social matrix. A recent finding of mirror self-recognition in a magpie (Prior, Schwarz, & Güntürkün, 2008), a member of the highly social corvid (crow) family with demonstrated impressive cognitive skills (Emery & Clayton, 2004) is consistent with this social intelligence hypothesis. Gallup seemed to anticipate the emerging discussions of the social factor in the development of a self concept in his conjecture that "self-awareness and mind are a product of selective pressures resulting from... intraspecific competition coupled with the need for cooperation (Gallup, 1982, p. 217)."

Rochat and Zahavi (2011) affirmed Gallup's claim that conscious experience presupposes self-awareness and that reductionist parsimony may fail to explain much of the large body of data accumulated from MSR studies, but at the same time they take exception with some of Gallup's other interpretations of the mirror test. They cite evidence from studies of human cultures with no prior experience with mirrors in which the initial exposure of individuals to their specular double invoked wariness, a response these authors claim may actually be universal across cultures, as when an individual is momentarily unsettled or even startled when unexpectedly encountering his or her mirror image. Rochat and Zahavi also question whether, for animals, the specular image corresponds to an internal model of the self. They suggest that more parsimonious explanations for MSR remain, such as a mapping of kinesthetically experienced body regions onto the mirror image by touching the corresponding mirror-image body parts (also see Mitchell, 1997). However, as was the case for explanations of animal metacognition, reductionist parsimony may not accommodate the vast amount of data that has been collected on MSR. Further, were simpler accounts that MSR involves a some gradual learning process true, such as kinesthetic-visual matching, would we not expect many animal species other than the few so far verified to be capable of MSR, particularly the various species of monkeys? Thus, an adequate theory must account for the failures of MSR as well as the successes. Empirical failures, such as failures to demonstrate MSR in some species, such as monkeys, can be validated or overturned through replication and careful attention to procedures and controls. Thus, dozens of studies of monkeys affirm the failure of MSR in this group. In contrast, early studies of MSR in dolphins (e.g., Marten & Psarakos, 1995) led to constructive criticisms (e.g., Anderson, 1995) that were later incorporated into more convincing demonstrations (Reiss & Marino, 2001).

7. Body and self

A view of the conscious self that has gained considerable traction in the literature is that of embodiment—the subjective experience of having and using a body, the sense of the self as located in the body, the body as experienced both objectively and subjectively as "my body" (e.g., Arzy et al., 2006; Bekoff & Sherman, 2004; Blanke & Metzinger, 2009; Eilan, Marcel, & Bermúdez, 1995; Synofzik, Vosgerau, & Newen, 2008) and represented consciously in a "body image" (Gallagher, 1986, 1995, 2009). Bermúdez (2009) points out that those philosophers who view the self as essentially embodied express that we have knowledge of our bodies "from the inside" through somatic proprioception. Somatic proprioception, Bermúdez contends, "provides a broadly perceptual awareness of the limits of the body as a physical object responsive to the will, and hence as clearly demarcated from other physical objects (p. 579)." More generally, Bermúdez holds that individuals are self-aware "relative to and as distinct from... other physical objects or other psychological subjects (p. 579)." Tsakiris and Frith (2009, p. 586) stress that "a principal quality of the self is grounded in the experience of the body as a sensory and motor entity," a

sense that one is the author of one's actions (sense of agency) and that the action is of one's own body (sense of ownership), concepts defined in detail by Gallagher (2000). Blanke and Metzinger (2009), define the simplest form of conscious experience of *self*, which they call "minimal phenomenal selfhood" as "the experience of being a whole, distinctive entity, capable of global self control and attention, possessing a body and a location in space and time (p. 7)." Arzy et al. (2006) state that "the sense of being localized within one's physical body is a fundamental aspect of the self (p. 8074)" and use EEG and evoked potential mapping to identify brain regions involved in mediating the self as embodied. Thus, for these various authors, an essential fundamental quality of selfhood is rooted in the body.

Several investigators have stressed that congruences between vision and self-directed movements in infants and animals are the product of a bodily sense of self rather than a conceptual sense (Ritchie & Carlson, 2010; Tsakiris & Haggard, 2005). Thus, a plausible conclusion from successful MSR tests with animals is that the subject recognizes that "that body is my body." The thesis of this paper is that this recognition is itself rooted in a more general sense of self as embodied in the conscious awareness of one's own body both objectively and subjectively as "my body." To this end, the sense of self, as manifested in a body image, and in the senses of agency and ownership of one's own actions, and possibly in mirror neuron systems that may promote awareness of self and of others, is rooted in the body in action (for some theories and reviews supporting this concept see e.g., de Vignemont, 2011; Jeannerod, 2003; Schütz-Bosbach et al., 2006; Sinigaglia & Rizzolatti, 2011; Synofzik et al., 2008; Tsakiris & Haggard, 2005). In the following sections I explore this thesis for the bottlenose dolphin for which a reasonable body of empirical and observational data exists relevant to this view.

8. Body Image and body schema

Gallagher (2009, p. 118) defined the body image as "a system of inconstant perceptions, feelings, and beliefs where the object of such intentional states is one's own body." Gallagher contrasted the body image with the body schema, defined as "a system of sensory-motor capacities designed for motor and postural control without awareness or the necessity for perceptual monitoring" (p. 118). He thus distinguished between a largely conscious perception of one's body and body parts as objects, yet experienced subjectively, from a largely unconscious system of proprioceptive and kinesthetic sensations and motor control. Thus, the conscious awareness of one's own legs (as "my legs"), as represented in a body image, is different from simply walking, which involves the body schema system. Earlier, Gallagher (1995), attempting to resolve some confusions in the literature on body schema and body image, emphasized that "the body image has an intentional status; that is, it is either a conscious representation of the body or a set of beliefs about the body" (p. 228). The concept of body image has been prominent in some expositions on the body and self-awareness (e.g., see various chapters in Bermudez, Marcel, & Eilan, 1995 and in de Preester & Knockaert, 2005).

Aberrations such as the sensation of a phantom limb experienced by some amputees can be thought of as the intact retention of the prior body image (Moseley & Brugger, 2009). In such cases, the phantom limb also remains part of the body schema; for example, after a leg amputation the individual may attempt to walk only to fall and realize that his leg is not really there (Gallagher, 1995). The plasticity of the conscious body image is also apparent in other cases, as in amputees whose phantom pain and phantom limb are eventually disowned, for instance by structured mirror viewing of their intact hand in the position of their phantom hand (Ramachandran & Rogers-Ramachandran, 2000), or by changes in somatotopic mapping after limb amputation, such as referrals of face stimulation to the phantom limb (Ramachandran & Rogers-Ramachandran, 2000), or by visual/somesthetic illusions experienced by intact participants in which simultaneous stroking of a visible rubber hand and one's own unseen hand leads to attributing the rubber hand to one's own body (Botvinick & Cohen, 1998) as well as the sensation of ownership of the rubber hand (Ehrsson, Spence, & Passingham, 2004). Also, with the sophisticated use of virtual reality techniques even out-of-body illusions can be created, in which the participant feels as if his location in space is that of a seen virtual body (Blanke & Metzinger, 2009; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). Thus, body image can be dynamic and mutable; components can be constructed and deconstructed under some conditions.

The partial loss of body-part awareness occasioned by certain types of brain trauma paradoxically provides further evidence for the authenticity of the body image construct and its distinction from the body schema. In "left neglect," for example, a condition associated with lesions in the right parietal lobe, the patient loses conscious awareness of the left side of the body while still maintaining conscious awareness and motor control of the right side (Coello & Delevoye-Turrell, 2007; Gallagher, 2009; Heilman, Watson, & Valenstein, 1985). Another example is autotopagnosia, a condition traced to lesions in the left parietal region (Ogden, 1985; Sirigu, Grafman, Bressler, & Sunderland, 1991) in which the patient is unable to locate the body parts being named by an examiner, either on himself, on the examiner, on a doll, or on a picture of a person. Semantic knowledge is not lost, however. If the examiner points to a body part, the patient can name it, e.g., "That is a knee." Conscious awareness and conscious control of one's own body parts thus seem dependent on the development of a representational body image.

9. Does the dolphin have a body image?

A study of a dolphin acting out instructions given by a researcher to move or use specified body parts in specified ways (Herman, Matus, Herman, Ivancic, & Pack, 2001) suggests that the answer is yes. In this study, the investigators assigned unique symbolic gestures (generally, noniconic gestures) to each of nine different body parts (Fig. 1: *rostrum*, *mouth*, *melon*,

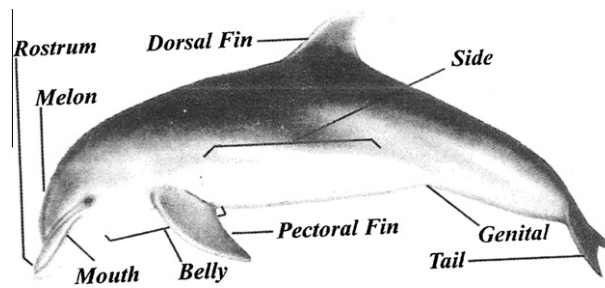


Fig. 1. Artist's rendering of a bottlenose dolphin showing the nine body parts referenced gesturally. Drawing by Barbara Stolen (courtesy of Sam Ridgway).

dorsal fin, side, belly, pectoral fin, genitals, tail) of a young female dolphin named Elele, by associating a unique gesture with each body part. After learning these associations, Elele was tested for her understanding of references to those body parts in the context of a sequence of symbolic gestural instructions asking her to use those body parts in specific ways—to either *show* the named body part (display it out of water), or *shake* it, or use it to *touch* a named object, or use it to *toss* a named object (Elele was taught the gestural names for various objects and actions during earlier studies). A key element of the test was whether Elele could use a named body part in a variety of ways, some of which were *novel* to her normal behavioral repertoire—actions that went beyond any natural or trained behavior and that were in some cases first occasions of an action. Overall, Elele was 90% correct over 10 trials in which she was asked to show a named body part and 80% correct over 20 trials in which she was asked to shake a named body part. She was correct on 85% of 196 trials in which she was asked to touch a named object with a named body part (there were several named objects floating about her pool, or fixed to the pool wall, or suspended above the water surface, so Elele had to select only the object referenced). Tossing a named object with a named body part was more difficult, as might be expected, but Elele still succeeded, significantly so, on 68% of 50 trials (conservatively, chance success was 0.11). Many of the requested behaviors were novel in the sense described, for example touching a floating Frisbee with the dorsal fin or tossing a floating surfboard using the genital area. Thus, in response to the instruction glossed as *Frisbee—dorsal fin—touch*, given as a rapid sequence of three symbolic gestures, Elele swam to the floating Frisbee (one of several objects having names floating about in her pool), turned her body lateral to it, and then carefully rotated her body so that her dorsal fin gently touched the top of the Frisbee (Fig. 2).

And, in response to the three-item gestural sequence *genitals—surfboard—toss*, Elele turned on her back, swam belly up to the floating surfboard, stopping there when her genital region was almost directly underneath, and with a vigorous upward thrust of her ventrum tossed the surfboard into the air (Fig. 3). When carrying out body-part instructions like these, Elele in effect had to answer a series of self-referring questions: “Which body part do I use; where, or on what do I use it; and how do I use it?”

These studies with Elele demonstrated that she was able to associate *different* gestural symbols with *different* body parts; that she could use the *same* body part in *different* ways, as instructed (e.g., shake your pectoral fin” versus “touch the ball with your pectoral fin”); and she could use *different* body parts in the *same* way (e.g., “touch the basket with your rostrum” versus “touch the basket with your tail”). These latter two criteria: the same body part in different uses, and different body parts in the same use, seem critical for demonstrating referential understanding of body-part names.

Comparatively, children as young as two can point to as many as 20 different body parts on a doll (MacWhinney, Cermak, & Fisher, 1987) or on themselves (Witt, Cermak, & Coster, 1990) in “show me” games, and can follow verbal instructions to



Fig. 2. Video frame from video sequence of the female dolphin Elele in the body-parts paradigm responding to the three-item gestural instruction, *Frisbee +dorsal fin +touch*. In response, Elele must swim from her instruction station, find the Frisbee, and then lay her dorsal fin on top of it. Multiple objects are present in the pool. Dolphin instructor: Elia Herman.



Fig. 3. Video frame from video sequence of the female dolphin Elele in the body-parts paradigm responding to the three-item gestural instruction, *Surfboard +genitals +toss*. She must swim from her instruction station, find the surfboard, turn on her back underneath it, and then toss the surfboard with an upward thrust of her genital area. Multiple objects are present in the pool. Dolphin instructor: Elia Herman.

use a body part in a specific way (e.g., “wash your hands,” or “wash your face”). Among animals, language-tutored chimpanzees have been taught gestural names for several body parts in some cases, but there appears to be no systematic study of their understanding of those parts referentially in a manner similar to that used with the dolphin Elele. Thus, of a corpus of over 600 verbal instructions given to the bonobo Kanzi, only about 10 included a body-part reference (Savage-Rumbaugh et al., 1993). Of those few, the references were usually to the body parts of others (e.g., “brush the doggie’s teeth”) and were generally context-limited or accompanied by prompting. Similarly, Terrace (1979) listed only five body-part names within the chimpanzee Nim’s receptive vocabulary of 200 items, but provided no data on the level or kind of understanding achieved. The gorilla Koko (Patterson & Cohen, 1994) reportedly could respond to the spoken words “eye,” “head,” or “nipple” by touching that body part or by giving the gestural symbol for that part, but no formal tests of understanding were given. This is not to say that apes might not be capable of understanding body parts referentially or of using them in novel ways when instructed, but that it has not yet been demonstrated.

What can be inferred about body image and consciousness from Elele’s ability to use her named body parts in the various specified ways? If a human were asked to carry out analogous tasks, including some that were novel or difficult (even silly?) body-part instructions (e.g., “toss the ball with your elbow” or “touch the door knob with your chin”), subsequent verbal report would certainly support that the individual was consciously aware topographically and semantically of the referenced body parts and consciously controlled them and, of course, was equipped with an understanding semantically of the object and action references. Thus, given the (hypothetical) similarity of dolphin and human responses in this body-part task, does parsimony lead us to accept that Elele had conscious awareness and conscious control of her body parts, as was similarly argued by Smith (2009) and Browne (2004) for attributing some level of consciousness to animals in metacognition tasks, based on human and animal functional similarities? Of course, for the dolphin, as for the human, there are many basic cognitive components or processes that support effective functioning in the body-part tasks, such as working memory, decision-making, planning, representation, and semantic processing. The instruction “surfboard, genitals, toss” had never been given Elele before, nor had any instruction requiring her to use her genitals to toss an object. How then did she construct her response and execute that instruction (as well as many others) if not through these types of mechanisms and conscious representations of her body parts?

Elele appeared to show body-image plasticity in her incorporation of semantic references to body parts that she may never have objectified previously, as, for example, the use of the melon to touch or toss an object. The “melon,” a body part specifically named for this study, is an amorphous area on top of the head in front of the blowhole, not visible to the dolphin, that encapsulates a lipid substance that functions principally to direct outgoing sound in echolocation tasks. It is not clear that a dolphin would have a previous structural representation of that body part, any more than we might have a structural representation of our vocal cords. The subsequent incorporation of that body part into the dolphin’s body-part repertoire, as evidenced by its ability to now use the melon in various ways, demonstrates the plasticity of the dolphin’s body image.

A final point in support of the consciousness hypothesis is that all of the many body-part instructions given the dolphins were in effect *transfer tests*, in which the dolphin apparently used a relatively sparse previously trained or experienced repertoire of body parts and related actions (e.g., Mercado, Uyeyama, Pack, & Herman, 1999) to form an expanded concept of body parts and their functional possibilities. By using her many body parts in many different ways, low-level explanations for her performance are excluded. Instead, some level of consciousness is a favored explanation, analogous to the transfer-test criterion put forth by Shea and Heyes (2010) for assessing animal consciousness in metacognitive tasks.

10. Agency and ownership of actions and the body as a basis for consciousness of self

In a seminal article, Gallagher (2000) distinguished two conscious components of self-initiated intentional movements: (a) the sense of *agency*—the sense that I am the cause or author of the movement, and (b) the sense of *ownership*: the sense that I am the subject of the movement (“it is *I* that is moving”). If someone pushes you, the sense of agency is negated but the sense of ownership is preserved (“It is my body that moved”). The senses of agency and ownership are instantiations of a form of conscious bodily awareness that recognizes self-produced movements and discriminates one’s own body and body

parts and their movements from those of others (Jeannerod, 2003; Tsakiris, Schütz-Bosbach, & Gallagher, 2007; also see later section on mirror neurons). Distortions of agency and ownership can occur, and like the example given of a loss of body image, serve to strengthen the concepts. For example, the alien hand syndrome (anarchic hand) reflects a failure of agency relative to that body part in which complex movements of the alien hand are not voluntarily initiated, as if the hand had “a mind of its own” (Scepkowski & Cronin-Golomb, 2003). Perceived ownership of the hand is intact, however, as are its normal sensations. Distortions or disruptions of the sense of agency may also underlie schizophrenic delusional thought and action (someone or something else was the author of my thoughts or my movements) (Cermolacce, Naudin, & Parnas, 2007). Behavioral studies manipulating self-movements and perceived effects suggest that the senses of agency and ownership are independent of each other (e.g., Sato & Yasuda, 2005), and brain studies confirm that sensory-motor processes that may be involved in the senses of agency and ownership are modulated by separate areas of the brain (e.g., Farrer & Frith, 2002; Tsakiris et al., 2007). Tsakiris et al. (2007) suggest that the senses of agency and ownership and efferent information induced by one’s own self-produced movement are important for self-recognition and self-awareness and not just for motor control.

Some recent discussions have emphasized the role of conscious awareness of one’s own body and bodily actions in the development of a sense of self. Kinsbourne (1995, p. 220), for example, stated, “As soon as the infant becomes able to focus attention on its body parts and their internally causally coherent behavior, it is equipped to develop a sense of self.” Stern (1985) lists the sense of agency, authoring one’s own actions, as one of the components of the “core sense of self” emerging over the first 6 months of life. Povinelli and Cant (1995) commenting on mirror self-recognition in the great apes and humans (the Hominoidea) proposed that awareness of self grew out of the requirement of the ancestors of the Hominoidea, brachiating species of increasing body size throughout evolution, for developing elaborated representations of their body, its mass, and its actions, as they traversed through branches of uncertain strength (also see Barth, Povinelli, & Cant, 2004).

11. Evidence for the senses of agency and ownership in dolphins: “self-imitation” studies

Barth et al. (2004) suggested that *only* the great apes and humans develop an elevated knowledge of their body as an object in itself. However, the research presented in Section 9 describing a dolphin’s referential understanding and use of its body parts as instructed by gestural commands demonstrates body objectification in a species unrelated to the Hominoidea. Is there also evidence that dolphins have a conscious sense of themselves as agents and owners of their actions? We addressed that question through research asking whether a dolphin can monitor its own actions well enough to repeat them again, or alternatively not repeat them, with each condition, *repeat* or *don’t repeat*, governed by unique gestural instructions from the experimenter. Because the dolphin is monitoring and copying its own actions (or not), we called this paradigm *self-imitation* (Herman, 2002). Custance, Whiten, and Bard (1995), in a replication of earlier work of Hayes and Hayes (1952), asked a chimpanzee to copy the motor behaviors of a human demonstrator in response to the verbal command, “Do as I do.” Self-imitation may be conceived of as a command (however given) to “Do as you did.”

In an initial set of studies (Mercado, Murray, Uyeyama, Pack, & Herman, 1998; Mercado et al., 1999) the dolphins Elele and Hiapo were taught the meaning of a hand gesture glossed as *repeat* that asked the dolphin to do again what it just did. The experimenter first directed the dolphin to perform some particular behavior, using the hand gesture that referenced that behavior. When the dolphin returned to its instruction station after carrying out the behavior, the experimenter might sign *repeat* or, alternatively, might give a sign directing some specific other behavior. For example, if the dolphin was initially instructed to perform a porpoising leap, on return to its station it might see the *repeat* gesture or, alternatively, a gesture asking for, say, a back swim (swim around the pool belly up).

After training the dolphins in the task using a limited number of exemplar behaviors, the dolphins were tested using a variety of additional behaviors, only some of which were followed with the *repeat* gesture. Some initial behaviors requested were new to the dolphins’ experiences, comprised of combinations of particular behaviors. Not knowing in advance which actions were to be repeated, the dolphins had to maintain a representation in working memory of the action just performed until further instructed gesturally (some conditions minimized or excluded proprioceptive or kinesthetic memory). Retrieval of that memory would seem to be a conscious act. By analogy, if a human were asked to “do (or say) that again” the individual must consciously (intentionally) access the representation of the last behavior from working memory before acting, clearly an act of volition. Attributing the same volitional control to dolphins would be parsimonious in the same sense as argued for metacognition studies that see clear parallels between human and animal strategies and responses.

In the Mercado et al. (1998) study, Elele correctly repeated her initial behavior on 114 (89.8%) of 127 *repeat* trials, comprised of 32 different behaviors tested four times each in a quasi-random sequence. Hiapo correctly repeated 62 (56.9%) of the 109 *repeat* trials he was given (chance probability was, conservatively, 0.125). Errors on *nonrepeat* trials were rare: 2% for Elele and 10% for Hiapo. Some examples of behaviors repeated successfully by both dolphins were swimming belly-up in a wide circle while waving the pectoral fins, blowing bubbles underwater, and touching an object with a pectoral fin.

In follow-on tests with Elele, she was also able to successfully repeat a behavior she herself had selected (her selection was directed only by the gesture “create” that asked her to take any initial action she chose (Braslau-Schneck, 1994 as reviewed in Herman, 2002)). Elele was also able to repeat an experimenter-directed behavior a second time, if the *repeat* instruction was given twice in a row. These latter two results supported the idea that Elele was accessing a representation of her past action, and not a representation of the gesture that had elicited that action. Mercado et al. (1999) showed that

Elele could also repeat previous actions taken to objects rather than just the movement patterns used in Mercado et al. (1998), showing that Elele's memory for past actions also incorporated representations of objects or locations of objects.

Further *repeat* studies with the dolphin Akeakamai showed that she could successfully repeat behaviors at better than 90% accuracy after delays up to 15 s and at better than 70% accuracy after delays up to 90 s (Cowan, 2003). Delays were of variable length so that Akeakamai could not anticipate when the delay period would end or whether the succeeding instruction would be to repeat her action or to do some other action specified by the instructor. During delays, Akeakamai remained at her station facing the experimenter, patiently waiting for the next instruction. During some delays, Akeakamai appeared to be overtly rehearsing her prior behavior, such as gently sculling her pectoral fins after having performed a “butterfly swim” that required her to swim on her back while waving those fins. Sculling while waiting did not occur after any other behavior. On the other hand, there were subtle behaviors during the waiting period that were common to *all* previous behaviors, such as small head movements after performing a “head shake,” but also after she had slapped her tail on the water or executed a somersault or a twisting jump. Thus, overt rehearsal was not a general strategy used by Akeakamai. Her ability to repeat her behavior after a delay even in the absence of overt rehearsal suggests the maintenance of stable mental representations of the behavior.

Self-imitation as witnessed in this *repeat* paradigm is consistent with an attribution of self-agency and self-ownership to the dolphins, with awareness of the functional properties of these states also implied. This is perhaps best illustrated in cases in which Elele self-selected a behavior in response to an instruction to “improvise” and then successfully repeated that behavior (in prior work, Braslau-Schneck, 1994, summarized in Herman, 2002, showed that that the dolphins Elele, Hiapo, Phoenix, and Akeakamai were all capable of innovating a wide variety of behaviors in response to the gestural command “Create.”).

A sense of agency and ownership can be demonstrated more compellingly if the dolphin can access the representation of its last behavior to *selectively* construct its next behavior to be the same as or different from its previous behavior, in effect choosing to do or not do what it did before. To gauge this ability, the female dolphin Phoenix was taught the meaning of both the *repeat* gesture and a different gesture glossed as *any* (Cutting, 1997; also see summary in Herman, 2002). The *any* gesture asked Phoenix to perform any action different from the one just executed, but all actions, either those directed by the instructor or those self-selected by Phoenix, were constrained to a set of five: *over*, *under*, *pectoral-fin touch*, *tail-touch*, and *mouth* (open your mouth about an object), with each action taken to the same object (a Styrofoam float positioned in the water near the dolphin). A trial began with the experimenter signing one of the five actions by using the unique gesture associated with that action. After Phoenix completed that action she returned to her trainer who signed either *repeat* or *any*. Thus, if Phoenix initially touched the float with her tail in response to the *tail-touch* instruction, she must do that again if instructed *repeat*, or self-select and carry out any one of the four remaining actions (*over*, *under*, *pectoral-fin touch*, or *mouth*) if instructed *any*. This procedure was repeated two more times, for a total of three *repeat* and/or *any* trials following the initial directed action. Phoenix was only rewarded if the entire sequence was executed correctly. An example from the study was Phoenix's successful response to the four-item sequence *pectoral-fin touch—any—repeat—any*. Phoenix first touched the float with her pectoral fin, then leaped over the float, then leaped over again, and finally touched the float with her tail (Fig. 4). To be successful in this task, Phoenix had to maintain a representation of her last behavior in working memory, update that as each successive behavior was performed, semantically process the succeeding instruction of *repeat* or *any*, and access the maintained representation of her last behavior, all in order to self-select her next behavior.

Altogether, there are eight three-way permutations of the repeat and any gestures (*any—any—any*; *any—any—repeat*; *any—repeat—any*; *any—repeat—repeat*; *repeat—repeat—repeat*; *repeat—any—repeat*; *repeat—repeat—any*; *repeat—any—any*) and each was



Fig. 4. Video frame from video sequence of the female dolphin Phoenix in the *repeat—any* paradigm. Phoenix begins each trial facing the instructor, who signs one of five action commands that Phoenix must take to the foam cylinder to her left. After performing the action and returning to the instructor, Phoenix sees either the gestural command *repeat*, asking her to do the same action again or, alternatively, the gestural command *any* asking her to choose a different action from among the four remaining possible actions of the set of five. This is repeated twice more and Phoenix is rewarded only if completing the entire sequence correctly. The *repeat* gesture is a quick movement of the right forearm outward from the stomach and back again; the *any* gesture is a quick extension of the entire right arm from the shoulder and back again. Dolphin instructor: Becca Cowan.

tested in random order from 79 to 81 times. Of the total of 638 sequences given, Phoenix responded wholly correctly to 585 (92%). During this task, Phoenix was hypothetically aware of her own actions, not just in the sense of ownership (“it was my body that acted”), but also in the sense of agency, especially in those cases in which she self-selected her own behavior following an *any* instruction (“I must author a different action”). These results with Phoenix thus extend the findings with Elele, Hiapo, and Akeakamai tested on only the *repeat* paradigm to show some of the cognitive underpinnings necessary for these tasks, including not only the semantic processing of the abstract concepts of *repeat* and *any* but also the processing semantically of the referents of each of the action commands that initiated a sequence. In an earlier section, following on Shea and Heyes (2010), I referred to successful transfer tests as an indicator of consciousness in metamemory tasks. The same criterion might be applied here by considering each of the unique *any-repeat* sequences as a transfer test. Sequences were different from one another not only in their different permutations but in the initial starting action requested by the trainer, or in some cases, by a request that the dolphin choose its own initial act if the trainer began a sequence by signing *any* (interestingly, in such cases, Phoenix generally hesitated, as if lost in indecision, before finally executing an initial action, the type of “uncertainty” behavior that Smith et al., 2003 suggests is mediated by “working consciousness”). To be successful in the *any/repeat* paradigm, Phoenix had to apply to each new sequence the concepts attached to *any* and *repeat* and the operations of maintaining, updating, and accessing stored representations in working memory of immediately past actions in order to make self-directed decisions about succeeding actions. Motor programs for executing each of the stored actions are also involved. Thus, there is nothing rote about the task. Instead, it appears as if the representation of the immediately past action as well as representations of possible future actions must be some of the dynamic contents of the dolphin’s conscious state, or what Smith et al. (2003) might call its working consciousness.

Griffin (1981) asked whether animals are aware of what they are doing. In answer, these findings on self-imitation by Elele, Hiapo, Akeakamai, and Phoenix give evidence that these dolphins not only understood what they *are* doing when executing an action, but also understood what they *were* doing in the immediate or recent past, using that information (however represented) as a basis for selecting their next action. More generally, Griffin (1992, 2001) concluded that since most are willing to grant that animals are aware of an act of others and are aware of others as actors, it is likely that they are aware of themselves as actors. Hence, “self-awareness seems a natural extension of granted perceptual consciousness: unless the range of objects and events the animal can consciously perceive is very narrow, the animal’s own body and its own actions must fall within the scope of its perceptual consciousness” (Griffin, 1992, p. 248).

12. Mirror neuron system: distinguishing self and other, and facilitating social imitation

As was reviewed earlier, neurological studies of monkeys and humans have uncovered specialized mirror neurons or mirror systems that are activated when performing an object-directed action (transitive actions), or when watching someone else perform that action “unifying action perception and action execution” (Rizzolatti & Sinigaglia, 2010, p. 264). Humans, but not monkeys, also respond to actions not directed toward an object (intransitive actions), such as meaningless arm waving (Rizzolatti & Craighero, 2004). Thus, one hypothesized function of the mirror neuron system is as an aid to understanding perceived actions of others “from the inside,” through the expression of corresponding motor representations in the observer’s brain (Rizzolatti & Sinigaglia, 2010).

A second proposed function is to facilitate social imitation (Rizzolatti et al., 2001) and social cognition (Schütz-Bosbach et al., 2006). “Action mirroring” suggests that social imitation “involves mapping of another’s actions onto the observer’s own motor representations” (Tsakiris et al., 2007, p. 655; also see Miall, 2003; Rizzolatti & Craighero, 2004), in effect adopting the other’s point of view. Social imitation, a key human attribute for the spread of cultural traits, is also a mechanism for the spread of cultural traits or behaviors among cetaceans (Rendell & Whitehead, 2001).

Sinigaglia and Rizzolatti (2011) distinguished between motor mimicry of simple behaviors having no goal object (“movement mirroring”), such as seeing someone simply extending an arm, and “action mirroring” involving a goal, such as observing someone extending an arm to grasp a cup. These authors contend that both movement and action mirroring depend on the mirror mechanism but in action mirroring the motor goal is seemingly encoded within the motor-evoked potentials. The authors emphasize that there is no evidence for movement mirroring in monkeys (see confirming findings of Visalberghi & Fragazy, 2002) but overwhelming evidence for its existence in humans. There is also overwhelming evidence for its existence in dolphins and chimpanzees (Herman, 2002).

In social imitation, as manifested overtly in behavioral or motor mimicry, the observer attempts to copy the *form* rather than the *purpose* of the behavior. Movement mirroring and its external behavioral expression through motor mimicry may be an evolutionarily adaptive trait enacted in complex societies in which alliances among individuals are of great importance and in which social imitation can serve as a signal of individual or group affiliation (“I’m like you” or “I’m with you”). In human societies, conscious or unconscious mimicry of facial expressions, emotions, motor behaviors, or dress codes can be signals of affiliation or empathy with the observed individual or group (Chartrand & van Baaren, 2009) and can affirm or strengthen relationships. Also, for humans, with all of our nuances of behavior, mimicry can sometimes be a sign of aggression, contempt, or “down-putting” of another individual, as in verbal or behavioral mockery.

Behavioral mimicry seems to be an innate process in humans as it is present even in neonates (Meltzoff & Moore, 1977). Synchronic imitation (Asendorpf, 2003) in which two children attend to each other with positive affect while engaging in simultaneous play in a similar way with similar objects emerges in the second year of life and may be an early manifestation

of imitation as a sign of social affiliation. According to Hart and Fegley (1994) social imitation by the preverbal infant is fundamental to the construction of a mental model of self, including both objective self-awareness and a distinction between self and other. In dolphin societies, synchrony of behaviors among pairs of animals or within small groups is common, especially among allied males, and has been viewed as an affirmation of social bonds (Connor, Smolker, & Bejder, 2006), a type of social signal not found among nonhuman primates (Connor, 2007). What then is the evidence for behavioral mimicry in dolphins and what does it imply about the dolphin's sense of self and other?

13. Social imitation by dolphins as evidence for consciousness of self and other

The bottlenose dolphin (and likely other cetacean species) is a superb imitative generalist, capable of both exact yet varied vocal mimicry (Reiss & McCowan, 1993; Richards, 1986; Richards, Wolz, & Herman, 1984) and versatile motor mimicry (Herman, 2002, 2006; Herman, Pack, & Morrel-Samuels, 1993; Xitco, 1988), a dual capability that dolphins have developed to a degree not found in any noncetacean species other than the human. Vocal mimicry of arbitrary electronically generated sounds has been demonstrated in the laboratory: The imitative vocalizations of the dolphin Akeakamai corresponded with remarkably little deviation from the frequency-time contours of the “model” sound heard by her (Richards et al., 1984, Fig. 2). In the wild, each dolphin develops a unique whistle sound, or “signature,” generally distinct from other dolphins in its group (Caldwell & Caldwell, 1965; Caldwell, Caldwell, & Tyack, 1990; Sayigh et al., 1999), although convergence of signature whistles among mothers and sons (Sayigh, Tyack, Wells, & Scott, 1990) and among closely allied males has also been observed (Smolker & Pepper, 1999; Watwood, Tyack, & Wells, 2004). Unique signatures may function as individual identifiers, allowing social contact even when individuals are out of visual range of one another. Occasional mimicry of one dolphin's whistle by another has been documented both in captive dolphins (Tyack, 1986) and in wild dolphins (Janik, 2000, 2009; Tyack, 2000), possibly serving as an affiliative call to that individual or as a symbolic reference to it.

Studies of successful behavioral (motor) mimicry by an observing dolphin of the actions of another dolphin or of a human have also been demonstrated (reviewed in Herman, 2002; Herman et al., 1993). During these dolphin mimicry studies, the imitating dolphin observed the action of a demonstrator (the “model”), either another dolphin or a human (the human was viewed either live at poolside, or in-water with the dolphin, or on a television screen), and then if instructed to imitate by a unique gestural sign glossed as “mimic,” attempted to copy that action. To copy the form of the behavior of a model, the imitator must have access to its own body image, must have an accurate representation of the body plan of the demonstrator, must be able to map the demonstrator's body parts onto its own, and must account for variations of the model and itself in space or aspect. This mapping seems most straightforward and transparent when the dolphin is imitating the observed behaviors of another dolphin but is less obvious in cross-species imitation.

When imitating the human model, regardless of whether the human's actions are represented visually or motorically (cf. Buccino et al., 2004; Rizzolatti & Craighero, 2004) the dolphin must be able to translate observed human movements into motor plans (an *inverse* model, Miall, 2003; Oztup et al., 2006), creating analogies where necessary. The dolphins described in Herman (2002), for example, raised their tails in the air when the human raised a leg, waved their “mirror-image” pectoral fin when the human waved an arm, and “walked” in close synchrony with a human walking about the perimeter of its pool (Fig. 5) by standing erect on its tail on the pool bottom and “hopping” forward step-by-step by pushing off the bottom, as well as turning around to “walk” in the opposite direction when the human did so.

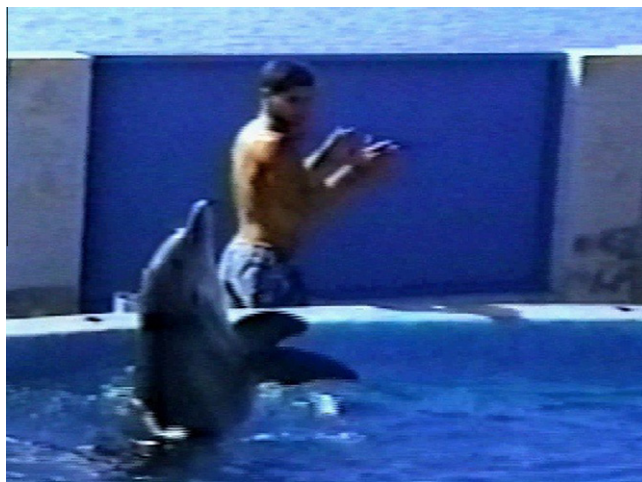


Fig. 5. Video frame from a sequence showing real-time imitation by the female dolphin Elele of a human demonstrator walking along the side of her pool back and forth and then leaping forward. Elele is moving forward by hopping along the pool bottom on her tail with her pectoral fins extended in copy of the demonstrator's extended arms. Demonstrator: Mark Deakos.



Fig. 6. Video frame from a sequence showing imitation of human actions by the female dolphin Phoenix. Phoenix, while stationed by her instructor views the behavior of an in-water demonstrator, and then if seeing the gesture glossed as *mimic* attempts to copy that behavior. In the first sequence, Phoenix views the demonstrator who is waving his arms (“body-wiggle”). Phoenix is then released to attempt an imitation by the *mimic* gesture, which is an up-and-down movement of the right arm tracing out an “M.” In the second sequence, Phoenix imitates the observer attempting to twirl a Frisbee. On some trials in this paradigm, Phoenix will not be asked to imitate but instead will be given a gesture directing some action different from the one demonstrated. Instructor: Becca Cowan. Demonstrator: Adam Pack.

An account of the mimicry experiments performed and the variety of behaviors imitated by the dolphin subjects is found in Herman (2002; also see Herman et al., 1993; Xitco, 1988). In one study, two dolphins, Phoenix and Akeakamai, each acted as the demonstrator for the other and, additionally, each attempted to imitate a human demonstrator who was in the water with them (Herman, 2002, Table 3.6). Of eight behaviors demonstrated on separate occasions by a dolphin model and by a human model, seven were copied successfully by one or both dolphins in response to the dolphin model and six were copied successfully for the human model. The behaviors copied successfully by both dolphins for both models were a pirouette, spitting water at an object, twirling a Frisbee (Fig. 6), slapping the tail on the water (the human in-water demonstrator slapped his legs), and pulling a rope to ring a bell (the human pulled with his hand, the dolphin with its mouth).

These studies of social imitation, together with those previously reviewed on self-imitation, provide evidence for a distinction by these dolphins of self and other, suggesting that in selecting, planning, and executing self- or other-imitations a dolphin exhibits a sense of agency and ownership: It must be able to attribute an action to its proper agent (itself or another), as well as attribute ownership of the action to itself or to another. The dolphin thus knows the *who* and *what* in these imitation paradigms. Jeannerod (2003, p. 1) notes that “the distinction between self-generated actions and actions produced by other agents, and the corresponding ability to attribute an action to its agent... appear to be key functions for self-recognition” (p. 1). He then notes further that self-recognition is a prerequisite for establishing social communication with others. It may be that when an imitating dolphin attends to each of a wide variety of behaviors demonstrated by a model, most of which are within the motor repertoire of the dolphin, that an *implicit* attribution of agency and ownership to others develops.

Vocal and motor mimicry characterize wild dolphin societies and support the findings from laboratory studies. What mechanisms might support these imitative capabilities? At a cognitive level, as evidenced in the laboratory setting by the wide variety of behaviors or sounds imitated and by the control of the imitative response by an arbitrary gesture or sound, it is apparent that the dolphin develops a *concept* of mimicry and not just an associative linkage between observed events and its own responses (Herman, 2002). Perhaps the strongest evidence for this is the spontaneous ability of the dolphins to imitate live televised images of humans exhibiting various behaviors (Herman, 2002; also see Herman, Morrel-Samuels & Pack, 1990). At a more fundamental level, it may be that mirror systems underlie and support mimicry capabilities and social intelligence has been suggested for humans.

A capacity for imitation may not only facilitate social cohesion through social copying of another, but as was noted, may also play a part in the development and spread of a cultural tradition or technique (Rendell & Whitehead, 2001). A subgroup of dolphins in Shark Bay, Australia, for example, uses sponges as a tool to assist in foraging for hidden fish on the rocky substrate, a culturally transmitted innovative technique apparently originating with a single female “Eve” and passed on vertically from mothers to mainly female young (Krützen et al., 2005; Smolker, Richards, Connor, Mann, & Berggren, 1997). Whether the youngsters learn by imitation or through ancillary mechanisms such as stimulus enhancement or local enhancement (Zentall, 1996) remains to be determined.

14. Conclusions

This paper adopted the thesis that consciousness of self is a multi-dimensional concept (Burghardt & Bekoff, 2009), as has been discussed and debated by philosophers for centuries, but that one aspect is that of the embodied self, the self as rooted in bodily self-awareness, a sense of the self as located in the body and experienced both subjectively and objectively

(cf. Legrand, 2007a). Tsakiris and Haggard (2005, p. 388) noted, “There is a clear link between body-awareness and self-consciousness.” In particular, these authors emphasized the contribution of the sense of embodied agency to body-awareness and hence to self-consciousness. Similarly, Jeannerod (2003, p. 1) identified the senses of agency and ownership as “the main constituents of the experience of being an independent self. . . (and that) “self-recognition is largely dependent on recognition of one’s own actions.” Synofzik et al. (2008) also identified the senses of agency and ownership as central features of self-consciousness.

This paper began with the question, “What does a dolphin understand about its body and self?” The studies reviewed urge the conclusion that awareness of self in dolphins is extant and that the self is embodied. Through these studies it is apparent or suggestive that the dolphin has a well-defined representational body image, a sense of agency and ownership for its own actions, possibly an implicit attribution of a body image and senses of agency and ownership to others, mental schemes or processes for codifying, representing, and distinguishing self-actions and other-actions, and social-awareness as well as self-awareness as defined through extensive social-imitation and self-imitation abilities, respectively.

Body self-awareness also seems extant in findings by others of mirror self-recognition by dolphins (and by great apes, elephants, and magpies) in which an external specular body is in theory mapped onto the observer’s own internal body image and expressed actions, so that the observer implicitly recognizes that “*that* body is my body.” In the current studies, body self-awareness is not tied to an external reference, suggesting that the dolphin implicitly recognizes “*this* body is me.” In successful social imitation (motor mimicry), distinguishing self and other is paramount so that, implicitly, the dolphin seems aware that “*that* body is you.”

A difficult question is what the results may imply about levels of consciousness. From Griffin’s (2001) definitions and arguments, the dolphins would be granted both perceptual and body consciousness. Griffin viewed body consciousness as intermediate between perceptual and reflective consciousness. Extending body self-awareness and the senses of agency and ownership of actions to a dolphin is crediting it with an awareness of both its subjective self (the “I”) and its objective self (“the “me”) (Legrand, 2007a), and is in keeping with concepts contending that self-consciousness requires representing oneself as an object (e.g., Eilan et al., 1995).

I noted earlier that metacognition studies revealed an animal’s ability to access the state or content of its perceptions, memories, or knowledge. Such access might also be granted to the dolphins in the present studies. Thus, what is the subjective mental state or the contents of consciousness for a dolphin when interpreting a gestural reference to a particular body part and organizing a novel response with that part; or when accessing a representation of its past action in order to decide on a future action among alternative possibilities; or when observing a demonstration of a behavior by a human that it must interpret and respond to in terms of its own body plan; or when temporarily “lost in indecision” when asked through an “any” gesture to choose its own behavior? Must it not be consciously aware of its own current perceptions, its own recent actions; its own body plan; its perceptions of the body plan and ongoing behavior of another (dolphin or human)? Parsimony would seem to suggest that some level of consciousness is involved in shepherding the dolphins’ performances through these various paradigms (cf. Browne, 2004; Smith, 2009).

The studies reviewed also revealed some of the extensive cognitive processing required of the dolphins in support of their performances in the different paradigms, such as an understanding of the action referents of the symbolic gestures we glossed as “mimic,” “repeat” “any” and “create,” including an understanding at both the conceptual level (what the term means in general) and at the practical level (what the specific instance requires in terms of the immediate context). Another example is the understanding, perceptually and cognitively, of the structural and functional relationships between its own body parts (as represented in a body image) and the body plan of others, including successfully processing and responding to both live (veridical) views and video views of others.

Baars (2005) contended that neurological homologies in human and nonhuman species having “human-like brains and behavior” suggests that consciousness of one kind or another is a basic biological adaptation, is phylogenetically ancient, and is not an exclusive human evolution. Structurally, a plausible hypothesis from the findings of impressive motor mimicry (action imitation) abilities in dolphins, is that dolphins like monkeys and humans possess a mirror system or its functional equivalent (given the differences in dolphin and primate brain architecture), but in view of the dolphin’s capacity for imitating both transitive and intransitive actions, the system might more closely resemble that of the human than that of the monkey. Brain studies in living dolphins are rare, but have been done (for purposes other than mirror neuron assessment) with specially trained dolphins (Ridgway et al., 2006). There are, however, considerable technical, logistical, medical, regulatory, and even ethical challenges to such study (also see concluding remarks in Connor, 2010).

Finally, given the independent trajectories for brain evolution and its architecture in the dolphins and primates (Connor, 2007; Oelschläger & Oelschläger, 2009), and given, paradoxically, the expression of convergent cognitive and social traits in these two divergent mammalian groups (Herman, 1980; Marino, 2002), it was suggested earlier that the common evolutionary cloth binding these two groups is the demands of social living in complex networks of sometimes collaborating and sometime competing individuals, and in which identification and knowledge of the behavioral and social propensities of others is paramount. In such societies a strong sense of self and other might emerge as an adaptive trait. Knowing yourself and knowing others would be immensely beneficial, as expressed through self-recognition, self-awareness, body-awareness, and attributions of these traits to others.

Continued study of the exceptionally large brained, slow developing, long-lived, highly mobile, and highly social dolphin species could be broadly significant, in the least by potentially contributing to furthering an understanding that the paths to

intellect, communication, and a sense of self and other do not require an obligatory traverse through the primate path of evolution.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.concog.2011.10.005](https://doi.org/10.1016/j.concog.2011.10.005).

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