

The Distribution and Evolution of Animal Consciousness

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CHAPTER 1 Preliminaries of Animal Consciousness

Which nonhuman animals (hereafter: animals) are conscious? Many people distinguish first between primary consciousness – which includes awareness of percepts, sensations, immediate thoughts and so on – and higher-order consciousness – which refers to awareness of one's primary awareness, or “thought about thought” (Edelman, 2003). A number of experimental paradigms have been devised in recent years to identify higher-order consciousness in animals (particularly primates, cetaceans, and birds), but the study of primary consciousness is somewhat more elusive. In what follows, I will use the term 'consciousness' to refer to primary consciousness.

What does it mean to be a conscious animal? One oft-cited definition is the one Nagel invoked when he asked what it is like to be a bat (1974). An organism or a mental process can be said to be conscious if there is *something that it is like* to be that organism or to be undergoing that process; essential to consciousness is its phenomenal, experiential, or qualitative feel. All animals are, to some degree, capable of selectively processing and responding to environmental information, and very complex cognition can in theory occur purely mechanistically. For some animals, however, responding to the environment also involves *experiencing* the environment (or the cognitive processes involved in behavioral-guidance, or the behavioral output) in a perspectively subjective way. It is this first-personal element that forms my interest here: which animals are capable of qualitative experience, and which are more like natural robots?

In asking what it is like to be a bat, Nagel's point is that the perspectival character of consciousness renders the contents of one's consciousness (like that of a bat) inaccessible to others. His choice of bats was deliberate, for two reasons. The first is that bats, like us, are

mammals. Anticipating the question I here pursue, Nagel remarks that “if one travels too far down the phylogenetic tree, people gradually shed their faith that there is experience there at all.” The second reason is that bats possess “a fundamentally alien form of life,” involving – among other ecological differences – navigation of their environment based on sonar rather than visual information.

Nagel couldn't have known it at the time, but there's another reason why his choice of bats was fitting. Donald Griffin, the zoologist who had discovered echolocation in bats (and coined the term) some thirty years before would subsequently become the father of cognitive ethology, a field that incorporates theory from cognitive science into the study of animal behavior and entertains hypotheses about the mental lives and experiences of animals rather than dismissing such modes of inquiry as anthropomorphic or misguided. Griffin was a forerunner in the movement to take consciousness seriously qua scientific explanandum, a movement that was met with staunch resistance, both in the case of cognitive ethology (Griffin's 1984 *Animal Thinking* was once called “the Satanic Verses of Animal Behavior”) and in the sciences more generally (for history, see Mandler, 2003). Nonetheless, Griffin was pivotal in convincing many scientists (particularly ethologists) to consider consciousness from an empirical and theoretical standpoint in spite of methodological limitations, arguing that as a natural phenomenon it should be scrutinously examined rather than barred from discussion. The importance of examining consciousness with attention to its perspectival nature is also a recurrent theme of Nagel's work: as he puts it in *The View from Nowhere* (1986), “the subjectivity of consciousness is an irreducible feature of reality – without which we couldn't do physics or anything else...and it must occupy a fundamental place in any credible worldview.”

There are many who believe the first-personal nature of consciousness places it beyond

the third-personal explanatory scope of science. Some suggest that we will be able to close this 'explanatory gap' if we first can come to a neurofunctional understanding of the correlates of consciousness (e.g. Crick and Koch, 1998); others hold that the gap is, in principle, uncloseable (e.g. Chalmers, 1996). It is true that neither science nor anything else can bring us inside the mind of another, but we can still measure the effects that consciousness has on an organism from the outside. Cognitive scientists and psychologists have advanced experimental study of this sort by treating consciousness as a variable (Baars, 1988). That is, experimenters measure the behavioral and neural profiles of subjects while varying either a subject's state of consciousness or the contents of consciousness.¹ Philosophers contribute by proposing and evaluating conceptual models to interpret these experimental findings. Cognitive ethologists, in turn, provide the opportunity to extend these results to the animal kingdom by highlighting the sophistication of mental activity underlying certain behavioral processes.

My goal here is to address a specific question about consciousness – its distribution in the natural world – by taking an interdisciplinary approach. As our understanding of the neuronal correlates of consciousness is still weak, neuroanatomical considerations will not be pivotal in my argument.² Rather, I first use experimental evidence from psychology and cognitive science to put forth a hypothesis about behavioral indicators of consciousness. I then turn to evidence from animal behavior to derive a substantive conclusion about animal consciousness that ultimately validates the proposals of many cognitive ethologists, albeit on different grounds. All the while, however, my method of inquiry will be philosophical in nature, and I will attend to

1 I discuss examples of such experiments in chapter 2.

2 I will, however, consider comparative neuroanatomy as a metric against which to weigh my hypothesis. That is, we expect that the neural complexity of a conscious organism should far exceed that of a nonconscious organism. In presenting my conclusions about which animals are conscious in chapter 4, I briefly point out how the distribution of neural complexity in the animal kingdom is consistent with my argument.

questions about the phenomenal nature of consciousness as well as the ethical import of scientific conclusions involving the mental lives of animals.

1.1 The Significance of Animal Consciousness

Why pursue the question of animal consciousness at all? Maybe, as Crick and Koch (1998) argue, we won't be in a position to answer it satisfactorily until we can explain the substrates of consciousness. Or, as Dennett (1995) suggests, it might be prudent to evade the question altogether, for fear that knowing too much about our fellow animals would discolor our relationship to them. I think, in the first place, that we can proceed scientifically although we currently lack a mechanistic understanding of how consciousness functions by appealing to evolutionary explanations, and that determining which animals might be conscious would have a range of implications too important to ignore or treat lightly.

Most obviously, the question of animal consciousness could have profound impact on our current ethical, legal, and scientific policy involving animals. There appears to be an element of bad faith in acknowledging that a certain animal is capable of experiencing pain, fear or suffering in the same vivid way that we do and insisting nonetheless that the animal's interests are inconsequential. How (if at all) we should actually implement change to accommodate conscious animals is a question of enormous scope, though I try to provide some insight in chapter 5. I think, however, that there are also reasons to wonder about animal consciousness that are not so moralistic in nature.

One reason stems from philosophical curiosity: an understanding of animal minds, presumably, would inform our understanding of our own. What makes us distinct as humans, and what do we share with the animals – and which do we share them with? (Perhaps this gives us a

modern way of conceptualizing 'human nature.')

Science has been able to study phenomena like social behavior and self-awareness to this end, but consciousness has not received scientific attention until relatively recently.

This issue of scientific methodology provides another reason to take interest in the question of animal experience. Studying consciousness in humans relies on accurate verbal report, which is not a possibility in the case of animals, so it seems that any answer to the question of animal consciousness would be speculative at best. But although we cannot ask another organism about its putative mental life, we can propose empirical litmus tests for consciousness with theoretical justification by utilizing resources in experimental psychology, evolutionary theory, and cognitive ethology. The thought is that by taking an interdisciplinary approach, we can try to answer questions that science might otherwise leave unaddressed.

The last major reason for interest in this topic has to do with characterizing and explaining consciousness. Many thinkers conceptualize consciousness as something mysterious and perhaps even beyond our epistemological grasp (the 'hard problem' of consciousness). While I don't think that answers about animal minds will solve the hard problem, I do think that it can help bring us closer by deflating it somewhat. Treating consciousness as an evolutionary phenomenon, we can theorize about its function and the way it might perform that function – perhaps we will even have a better idea of why, in performing this function, we experience the phenomenal (and why there is a 'we' to experience it).

1.2 Consciousness and the Phenomenal

This brings me to an important point. There is a certain tension between the philosophical nature of the question I'm asking and the scientific means I intend to take to answer it. I took my

departure from Nagel's subjective 'what-it-is-like-ness.' The question I am asking is which animals are capable of such phenomenal experience, which is an essential part of consciousness. However, Block (1995) points out that consciousness (at least as the term is used in science) is not limited to its phenomenal, qualitative character – there is also a cognitive component.

Block proposes a conceptual distinction between phenomenal consciousness (the “technicolor phenomenology of conscious experience”) and access consciousness (“what Freud meant by consciousness”) (Blackmore, 2006). A mental process is a-conscious just in case the information it contains is available for verbal report, reasoning or executive control of action. Gray et al. (2007) show that this distinction is also latent in our intuitive judgments about other minds. For example, we typically take the minds of infants and of familiar animals (such as dogs or cows) to consist in a relatively high degree of experience (p-consciousness) with a relatively low degree of agency (a-consciousness).³

There is something to be said for this intuition. After all, our own a-consciousness, unlike that of animals, is pervasively linguistic. We might suspect that our language faculty would contribute substantially to our capacity for the conscious experience of propositional thought and furnish a higher-functioning access consciousness. Spelke (2003), for instance, discusses how language enables a more complex capacity for spatial cognition. Normal adult subjects can navigate using single spatial cues (e.g. “to the right of cylinder”) equally well in control conditions and when given a verbal shadowing task, in which they must repeat a series of words dictated to them. Navigation tasks involving more than one spatial cue (e.g. “to the right of the

3 I do not mean to suggest that the Block's access/phenomenal distinction aligns directly with Gray et al.'s agency/experience distinction, but I do think there is strong overlap. Questions correlated with experience focused on the phenomenal element of the animal's mental life (e.g. “can this organism feel hunger?”) while questions correlated with agency focused on the animal's executive mental capacities (“can this organism intentionally seek to satisfy its hunger?”), which are strengthened by an adept access consciousness.

cylinder that is behind the door”), however, become much more difficult when coupled with the shadowing task – presumably because such tasks necessitate the use of linguistic thought.

Similarly, a working language faculty contributes to tasks of categorization and conceptualization, as seen in the contrast of linguistic and non-linguistic species of birds. Most avian species can innately discern numbers with relative accuracy, and responses to numerical discrimination tasks typically fall on bell curves centered around the correct answer (Emerton et al., 1997). If, however, the bird has acquired linguistic labels with which to identify numbers, then its performance on such tasks becomes markedly more precise (Pepperberg, 2006).

Language appears to be an enabling faculty when it comes to executive control of behavior and of thought, and it seems probable that non-linguistic capacities for symbolic manipulation and conceptualization would also contribute to a more capable access consciousness. So, from an evolutionary standpoint, we might suppose that consciousness as it first arose was largely phenomenal in character, and that the first mental processes to be consciously experienced were sensory and bodily percepts. These animals would in some capacity experience the world and their own actions, but without executive distance⁴ from those actions (perhaps similar to what it feels like to be in a dream). Later in evolutionary time, with the development of further cognitive capacities, mental processes such as decisions, judgments and volitions might also 'rise to the surface' of consciousness. On this view, a-consciousness is not a phenomenon that occurs separate from p-consciousness, but rather represents certain types of mental processes that may be experienced – that is, that may be conscious.⁵

4 Phenomenally experienced information would still influence an organism's action, but this influence would be subconscious, as seen in priming (discussed at length in chapter 2).

5 Kihlstrom (1987) puts this point quite nicely: “One thing is now clear: consciousness is not to be identified with any particular perceptual-cognitive functions such as discriminative response to stimulation, perception, memory, or the higher mental processes involved in judgment or problem-solving. All of these functions can

I don't believe that questions about phenomenal experience are beyond the scope of science, although current research dissociating the cognitive and phenomenal components of consciousness is still in the early stages (for review, see Ellis and Newton, 1998). Research on primary human consciousness (*simpliciter*, without attention to this distinction), however, is markedly more advanced and still has potential for answering the question of animal experience. After all, consciousness in humans doesn't normally occur without the phenomenal element that I am targeting, and so we can identify the most probable candidates for conscious experience by providing an argument for which animals are conscious while operating within this scientific paradigm.

For the bulk of my argument in this thesis (especially the next chapter), I will be relying on evidence from cognitive science to advance an argument about indicators of consciousness in animal behavior. Accordingly, my argument functions within the scientific paradigm, and I use the word 'consciousness' to refer to the process of primary consciousness in normal human subjects – of which 'what-is-it-like-ness' is an essential component. I argue that there are a number of animal taxa that possess this form of consciousness, while a tenuous argument at best could be made for their immediate evolutionary predecessors. As the distribution of phenomenal experience or 'what-it-is-likeness' is presumably broader than that of consciousness, I put forth the speculation that these latter groups of animals might have some form of 'proto-consciousness,' which would be phenomenal in character and cognitively simplistic.

Although my argument employs a scientific model of consciousness that doesn't invoke Block's distinction, I will attend to the relation between consciousness and phenomenal experience. In particular, I ask how scientific conclusions regarding consciousness can inform

take place outside of phenomenal awareness. Rather, consciousness is an experiential quality that may accompany any of these functions.”

ethical discussion in chapter 5, operating under the assumption that there may be some 'proto-conscious' animals who experience phenomenal sensations but do not obviously fit the scientific metric for consciousness that I propose. I examine the assumption that phenomenal experience is a necessary condition for moral consideration, and also discuss the ways in which the gradation between this basic phenomenal experience and more sophisticated forms of consciousness – which may include consciously experiencing things like desires, plans, and a sense of self – might bear moral import. Additionally, in a footnote to chapter 3 I briefly suggest a way to explain the role of the phenomenal given the hypothesis about the function of consciousness I advance.

1.3 Methodology

Operating within a scientific context, how can we determine which animals are conscious? Churchland (2002) comments that there are two complementary investigative styles pertinent to consciousness, one direct and the other indirect. The direct (or “brain-friendly”) method involves studying the mechanisms underlying consciousness. There is still much work to be done in this area, and a comparative neuroanatomical approach moreover leaves open the fascinating question of whether consciousness could be realized in animals with radically different neurostructures (I am thinking of cephalopods in particular; see chapter 5 for discussion).

If anatomical evidence is insubstantial, we will have to rely on patterns of behavior (what Churchland calls the indirect approach). Some philosophers (e.g. Tye, 1997; Carruthers, 2002) suggest that conceptual analysis of consciousness can yield predictable observations about what behaviors consciousness should enable. Similarly, cognitive ethologists propose examples of

sophisticated cognition (typically involving problem-solving) from the animal kingdom that seem unlikely to occur without conscious effort. My approach differs from these in that it hinges directly on evolutionary considerations. That is, I will give a historical, rather than structural, explanation of consciousness and use this explanation to propose patterns of behavior that are indicative of consciousness.

I proceed from the assumption that consciousness is a product of evolution by natural selection. In chapter 2, I ask the question of whether it serves an adaptive function: what is it that conscious processes do that unconscious processes cannot? Following Bernard Baars, I answer that consciousness has the property of globally broadcasting information to a system of 'specialist modules' distributed through the brain. I elaborate on this notion in chapter 3, suggesting that this enables certain forms of associative learning. In chapter 4 I survey evidence of associative capacities throughout the animal kingdom in order to arrive at a conclusion to the question of the distribution of consciousness. I close by discussing the moral import of animal consciousness in chapter 5, and suggesting some issues (and possible solutions) in bridging the gap from scientific conclusions to ethical consequences.

CHAPTER 2

Towards a Function of Consciousness: Evolutionary Considerations and Global Workspace Theory

In this chapter, I situate consciousness in an evolutionary context: how and why did it arise? Was it a fluke of nature, some glitch in natural selection that took robotic organisms and endowed them with the capacity for experience? I refute this possibility in the first section, and in the second I argue in favor of a particular hypothesis about consciousness' function – which I refer to as the the 'broadcast hypothesis.' If we can determine what, evolutionarily speaking, consciousness *does*, we can begin to theorize about how it might manifest its presence in an organism's behavior.

2.1 The Evolutionary Status of Consciousness

How did consciousness come into the world? Here is one vague but probable story: approximately 1 billion years ago, multicellular life forms were synthesized from colonies of eukaryotic protozoa. Simple animals proliferated over the next several hundred million years, and with the Cambrian explosion 530 million years ago these animals became more diverse, numerous, and better adapted to changing environments. Selection pressures favored complex nervous systems that could translate input of environmental information into output of appropriate behavior for a wide range of situations. In time, some nervous systems became so complex that they enabled their possessors not merely to process and respond to the environment, but to consciously *experience* it. This trait was passed on from one generation to another, and its bearers fared well in the natural struggle. Briefly: consciousness evolved.

2.1.1 The Spandrel Possibility

The above story is neutral with respect to a number of questions. Did consciousness evolve just once, or multiple times along different phylogenetic branches? Did it evolve

gradually or was the transition from unconsciousness to consciousness more or less discrete?

Most crucially: was consciousness selected for some adaptive purpose, or was it a byproduct of the selection of other traits?

After all, not all phenotypes are the direct product of natural selection; an organism may have a trait or property that arose incidentally during the natural selection of some other, more adaptive, feature. These evolutionary byproducts are called 'spandrels', and a classical example is the redness of most animals' blood (Gould and Lewontin, 1979). The presence of iron-based hemoglobin in the blood was an adaptive trait because it allowed the blood to transport oxygen. But the red color of blood is not essential to this adaptation: the molecule selected to carry oxygen through tissues could have turned out to be any other color and still functioned identically.

It could be that consciousness – or some constitutive component thereof – is incidental in this way. It seems possible that if you give an organism sufficient neural complexity to do the sorts of diverse cognitive tasks our ancestors must have done, consciousness will supervene on the whole structure, without the immediate influence of natural selection. Is consciousness a spandrel, or does it serve some evolutionary purpose?

It is sometimes assumed that in order to prove that some trait is an adaptation, you must already know its function. If you first know what role a trait serves, then you only have to demonstrate that in performing this role, it enhances the organism's performance or survival somehow. This approach would be problematic in the case of consciousness. However, structural clues about a trait can serve as indicators of the presence of a function before determining what that function is (Grantham and Nichols, 2000). To take one instance, most fish have an organ called the lateral line that runs down their back. Although the function of this organ was

originally unknown, scientists ruled out the possibility that it was a spandrel by arguing that an organ with such a complex anatomy that shows constancy across multiple taxa could not be a mere fluke, for such complexity and precision is difficult to maintain (Brandon, 1997). It is now known that the lateral line is used for sensing water movement in order to detect the location and movement of other nearby organisms.

Consciousness is similar to the lateral line, in that it depends on structural complexity and precision to arise. Before saying exactly what this complexity and precision amounts to, however, I survey a few additional sources of evidence – some successful, some unsuccessful – for the claim that consciousness does have an adaptive function.

2.1.2 Evidence for the Adaptive Value of Consciousness

Typically, one establishes the adaptivity of a trait by comparing an organism that has the trait to one that doesn't: if the trait is adaptive, then the possessor organism should be more fit than the other. Such arguments by comparison are unavailable in the case of consciousness as we don't yet know which creatures are and aren't conscious. Another classical piece of evidence in favor of a trait's adaptive value is its costliness: if a trait is in some sense 'costly' to maintain, then we infer that it must serve some function, since natural selection will eliminate traits that impose pointless burdens on an organism. There are many ways to understand 'costliness:' a trait may, for example, decrease mating opportunities or increase the risk of predation. In the case of a mental process like consciousness, the most obvious sort of costliness would be metabolic. If we could determine that conscious mental processes (or the neural substrates thereof) require markedly more energy than their nonconscious analogues, we would have strong experimental evidence that consciousness is adaptive.

Despite the lack of conclusive empirical evidence for the adaptivity of consciousness,

there is strong theoretical evidence in its favor. This evidence stems from two sources: the phenomenon of attention, and from the notion of 'complexity' as invoked by scientists in the case of the lateral line.

All animals are at least minimally responsive to their environment. Most are further capable of directing their focus to one task or stimulus as necessary, but attention entails more than this: it involves a subsequent withdraw of focus from other stimuli. If you are in a room where there are multiple conversations occurring, by focusing your conscious attention on just one – that is, by mentally engaging in it – you will be able to perceive it more distinctly than the others (the 'cocktail party effect').⁶ If conscious processes do not have some special capability that unconscious processes lack, then it is puzzling why organisms would be able to pay attention selectively at the level of sophistication that we can. If consciously experiencing a stimulus doesn't affect information processing at all, then why would evolution subsequently refine our ability to direct our consciousness towards certain information sources and away from others?

Another, related piece of evidence for the adaptive nature of consciousness is its complexity. Conscious processes, unlike those unconscious, are *unitary* and *integrated*, reflecting the binding of input from multiple sensory modalities (Edelman, 2003). At any one moment, the content of one's conscious perceptual experience includes some combination of the five senses, bodily sensations like pain or heat, as well as emotions and dispositions. Propositional content like thoughts, judgments, volitions and beliefs may also be experienced consciously.⁷ The phenomenon of consciousness allows all of these informational inputs, which would otherwise be processed in parallel, to be integrated. We experience one conscious state at

6 The selectivity of conscious attention has been documented in other modalities as well, but is most palpable in its auditory form, owing perhaps to the human language faculty (Johnston and Dark, 1986).

7 Although, as previously discussed, the capacity for language presumably enriches one's conscious experience of such mental processes.

a time, but each conscious state consists in information from a number of different sources. This integration provides a necessary condition for the creation of a unified, constant 'self' that undergoes each of these conscious experiences.

Conscious mental processes exhibit an integrative complexity as well as a responsiveness to the executive control of attention that are improbable to have evolved by chance. Next, I ask: what was consciousness selected for – what advantage does it confer on its possessors? To answer this, we must isolate what can conscious mental processes do that unconscious mental processes cannot.

2.2 The Function of Consciousness

Consciousness need not have only one function, although until this point I have been discussing it as if this were the case. Biological adaptations tend to be accretive, and so it would not be surprising if consciousness turned out to serve several functions (Rozin 1976). Here, however, I am targeting consciousness' function more broadly: I am trying to isolate the essential capacity of conscious states that furnishes consciousness with its more specific capabilities.

2.2.1 Consciousness and Representationalism

We can get a rough idea of the function of consciousness by first taking a top-down approach. Conscious processes are, more generally, *mental* processes, and so we might suspect that conscious processes perform the general function of mental processes in some specialized way. Consider, for example, a ball-and-socket joint. Joints allow movement at the interface between two or more bones, and ball-and-socket joints perform this function in a particular way – they are structurally adapted to allow for rotation. Conscious processes are a subset of mental processes, so we might begin to approach their function by asking: what is the function of mental processes?

The brain does a lot with the information it receives. It can form propensities and aversions, acquire new skills, and store memories, to name a few. In order for the brain to process information acquired from the outside world, it must first encode that information to itself (Dretske, 1995). The technical term for this encoding is *representation*, with representationalism being the thesis that representation is the primary or most general function of the nervous system and of mental processes.

Representationalism has a long history in theoretical cognitive science and philosophy of mind. It derives from Brentano's thesis that intentionality is the “mark of the mental” (1874). Mental processes, Brentano argued, have the property of always carrying reference to something else – they are always *about* something, in the way that when I cut my finger the sensation of pain represents to me the presence of physical trauma. There is no such thing as a 'raw' or contentless mental state; all mental states correspond to something (such as an entity in the world, a proposition, or a disposition). As illustrated by misrepresentations (e.g. illusions or misperceptions) a mental state's content need not be accurate or veridical. But when we are conscious, our conscious mental processes must represent *some* content – indeed, depriving the brain of sensory input is one way of inducing hallucinations (Flynn, 1962).

Representationalism holds that mental processes, be they sensory or propositional in character, represent information. So we would expect that conscious states represent information in a particular way, that there is something privileged about their manner of representation. What does this privileged character consist in – how do conscious mental processes represent information differently from the way unconscious processes do? I approach an answer to this question by taking a comparative perspective, noting the functional differences between

conscious and unconscious processes.⁸ This is one application of what Baars calls 'treating consciousness as a variable.'

In terms of information processing, the structure of the conscious mind is radically different from the brain as a whole. Conscious states are unified, integrated and serial: they are presented in temporal succession, with each state constituted by information from multiple inputs. They are, however, also limited in their scope: full conscious attention can only be given to one task at a time, and dividing attention among multiple processes is difficult. (Consider how hard it is to actively listen to two conversations simultaneously, or even the difficulty most people face in trying simultaneously to rub their stomach and pat their head.) The unconscious brain is not limited in this way because it processes information in parallel. Since multiple pathways are not integrated, each of the pathways can process simultaneously. This means that the processing capacity of the unconscious brain at any one moment is drastically larger than that of the conscious mind.

2.2.2 The Capable Unconscious

This large processing capacity means that the unconscious brain is capable of directing remarkably sophisticated behaviors. We can do surprisingly much without paying conscious attention because the procedural knowledge necessary to perform familiar, automatic processes is unconscious. Once a behavior has been internalized through learning and repetition, we can perform that behavior even if our attention is directed elsewhere (Kihlstrom, 1987). A common example of unconscious access to procedural knowledge is driving a car. An experienced driver can be, as it were, unconscious of her surroundings: though her eyes are directed to the road, she

⁸ This comparative approach differs from the one dismissed in 2.1.2. There, I rejected the possibility of determining consciousness' function by comparing two organisms (one with and one without consciousness). Here, we hold the organism constant and compare two different mental states, one conscious and the other unconscious.

might be focusing on conversing with her passenger or deep in thought. She will nonetheless be able to drive around an obstacle in her way, but will not report any awareness of that task she just performed or of the obstacle after the fact. Similarly, when learning a new language, conscious attention to learned rules of grammar or vocabulary is detrimental; in order to speak fluently one must commit the rules of the language to unconscious memory. The same principle holds for acquired skills more generally: excessive conscious consideration of the task at hand undermines performance (Langer and Imber, 1979). We carry out such tasks skillfully when we loosen the grasp of attention on the matter at hand and act unreflectively. In this way, committing procedural knowledge to unconscious memory makes what Baars calls “canned solutions” automatically available in familiar situations (1988). There is also evidence that unconsciously made decisions often result in higher levels of satisfaction than those that involve conscious consideration (Wilson and Schooler, 1991).

Unconscious stimuli can direct our behaviors even when we are not performing a familiar task, because the unconscious provides context for and thereby shapes how the contents of consciousness are experienced (Baars, 1988). While unconscious context-setting occurs incessantly, we can gain insight into how it works by considering it under controlled circumstances through priming. Priming is a nonconscious form of memory which serves primarily to contextualize subsequent stimuli and shape responses to them. For example, in one experiment subjects are subliminally presented with randomly generated names. They are later presented with a list of names, some famous and some randomly generated. Subjects are more likely to (mistakenly) identify the names that were subconsciously presented to them as famous on the basis of their prior exposure. These kinds of effects induced by priming can last up to several weeks (Squire, 1992).

2.2.3 Limits of the Unconscious

Priming, however, only functions within certain parameters. As Murphy and Zajonc (1993) demonstrate, primes without affective valence – those unlikely to produce any significant reaction if presented supraliminally – must be presented repeatedly or for longer periods of time in order to have any affect on subsequent judgments. Furthermore, priming shows minimal modal flexibility: visual primes typically alter responses to visual cues, verbal primes typically alter responses to verbal cues, and so on. Tulving and Schacter (1990) call this limited capacity of priming 'hyperspecificity of access.' So, although unconscious presentation of stimuli can affect subsequent cognitive processing, these effects are limited in a way that conscious presentation of stimuli is not: the influence of conscious percepts upon subsequent cognitive processing is more universal and more flexible than that of unconscious percepts.

This point is further evidenced by the familiar phenomenon of blindsight, in which patients with occipital lobe damage have a blind gap (scotoma) in their visual field. Patients report no conscious experience of any stimuli presented within the scotoma. Information presented in the blind area is still available for subconscious cognitive processing, as evidenced by the above-chance rates at which patients are able to guess the characteristics of the stimuli within the scotoma. If this subconsciously processed information is to be employed, however, patients must always be prompted to guess (Stoerig and Cowey, 1997).

Context-setting, blindsight and priming are examples of what the unconscious intake of information can do. Unconsciously received information can shape subsequent judgments and affective states, for instance. But the effects of unconscious information are constrained: the information is available for certain pathways of cognitive processing, but not for others.

What is special about conscious states is precisely that they are *not* constrained in this

way. Conscious states are limited in their scope of input: we can only focus our conscious attention on a minimal number of tasks or stimuli at any given moment. But though less information can be taken in by conscious attention and processed at any one moment, the information that is taken in becomes much more widely available to different pathways of cognitive processing than in the case of unconsciously received stimuli.

2.2.4 The Wide Scope of Consciousness: The Broadcast Hypothesis

Mental states represent, and conscious mental states represent in a special way: they *broadcast*. That is, the information represented in a conscious mental state is available for processing by multiple 'specialist' modules in the brain. Information taken in unconsciously does not exhibit this wide availability: the information is processed only by certain modules that are typically associated with information of that form of input. It is for this reason that the effects of priming tend to be constrained to the sensory modality through which the stimulus was received, and that low-valence stimuli tend to produce little effect. Consciously experienced mental processes mobilize many unconscious specialized networks by broadcasting their contents.

The notion that conscious states 'broadcast' is, of course, a metaphor: we do not yet have a robust enough understanding of the physical substrates of information processing in the brain to say what conscious states do in materialistic terms. But before we can generate a science of physically testable hypotheses we must settle conceptual foundations that can be applied to the phenomena we observe. Accordingly, the broadcast hypothesis can be more clearly understood within its conceptual framework, that of the 'Global Workspace' advanced by Baars (1998) and approaching near-consensus in the scientific community (see, for example, Edelman, 1989; Kanwisher, 2001; Dehaene and Naccache, 2001; Edelman and Tononi, 2000; Damasio, 1989; John, 2001). On this view, the brain consists in a system of specialized networks that compete

for control of the 'workspace' of consciousness. Information that reaches the workspace is, in turn, broadcast out to the specialists to process and thereby made globally available.

Baars employs a theater metaphor to elaborate on this broadcasting function of consciousness.⁹ Consciousness, according to Baars, is like a small spot of light cast on the stage of a dark theater. The whole theater represents the brain: at any given moment, most of its processes are unconscious, just as the majority of the theater is dark. There is minimal interaction between these processes – for the most part, they operate in parallel – but the information in the spotlight area can be seen and therefore accessed by all of them, creating a 'global workspace' with which specialists can coordinate their efforts.¹⁰ Throughout the theater, there is constant processing of information, and some of this information loops back to the executive control mechanisms that in turn guide the spotlight of attention to focus on – and render conscious – different mental processes. In the dark on the stage are those brain processes which could potentially be conscious, which Morsella (2005) calls *consciously penetrable*, while the audience consists of those brain processes that are never experienced consciously, which Morsella calls *consciously impenetrable*. Baars proposes the cerebral cortex, hippocampus, basal ganglia and amygdala as likely members of this consciously impenetrable audience, which furthermore is not merely helping to guide the direction of the spotlight, but altering the presentation of what is

9 This theater metaphor is not intended to be taken in the sense of a dualist “Cartesian theater,” in which the metaphysical self sits apart from the workings of the brain like a homunculus looking in on the contents of conscious experience. The conscious self is not a spectator watching the spotlight. A better way to characterize the self on this metaphor might be to say that it simply *is* the spotlight, proceeding from one conscious experience to another, the trajectory of which is determined both by consciously experienced (spotlit) and unconscious processes. The argument between Dennett and Baars is primarily one of whether theater metaphors are more misleading than they are useful – although Dennett also wants to resist the Cartesian materialist notion that there is one physical locus in the brain to which conscious information is sent, and Baars (1997) appears to advocate something similar to this idea when he claims that Gazzaniga has found a 'narrative interpreter' in the frontal cortex. For a full discussion, see Rockwell, 1997.

10 It is not clear to what *extent* conscious information is broadcast; whether it is universally available but discarded by pathways with no use for it or whether it is only available to a restricted number of unconscious pathways. Or, it may be that some mental processes are broadcast less globally than others and are barely consciously experienced (“fringe consciousness.”) This question presumably hinges on further experimentation.

within it, as the contents of unconscious experience have a context-providing function (Baars, 1988).

The metaphor of the brain as a vastly distributed theater of experts and the conscious mind as a spotlight reflects the complex capacity that consciousness confers to an organism. Information from multiple pathways is integrated in the spotlight of consciousness, and this information is then accessible to a number of subsequent processes that feed back to control the context and contents of subsequent states of consciousness. In so doing, consciousness coordinates the functioning of many 'specialist' pathways that would otherwise operate autonomously.

2.2.5 Testing the Hypothesis: Evidence of Broadcasting

The different forms of memory provide a prime example of what it means for conscious states to 'broadcast' information. There are two major types of memory: declarative (explicit, “knowing-that”) and non-declarative (implicit, “knowing-how”) (Squire, 1992). Declarative memory consists in stored factual information and is distinguished by its reportability. It may either be semantic (i.e. memory of data or facts) or episodic (i.e. memory of events). In order for information to be committed to declarative memory, it must be consciously processed. For this reason, amnesiacs – whose capacity declarative memory is impaired – fail at rapidly forming novel associations (Squire, 1992).

Non-declarative memory, by contrast, may be processed subconsciously. It is unaffected in most amnesic patients, and includes procedural memory such as skills or habits, as well as simple classical conditioning and nonassociative learning. Information acquired through non-declarative memory is expressed through performance rather than through recollection.

Declarative memory is different from non-declarative memory in three ways: it is faster,

it is accessible to conscious recollection, and, crucially, it is *flexible* (that is, available to multiple response systems). Non-declarative memory is highly specific, meaning that information learned and stored via non-declarative memory is accessible only through the response systems involved in the original learning process (Cohen, Poldrack and Eichenbaum, 1997). (This is why, for instance, learning to write with one hand does not translate into any form of dexterity with the other.) Information stored by declarative memory, by contrast, can be accessed by a multitude of cognitive pathways because it is broadcast to those pathways.

Another illustration of the notion of broadcasting – one that allows us to observe its putative physical effects in the brain – is provided by habituation. When we are presented with an intrusive novel stimulus (say a sudden poke), it demands our attention: that is, we experience it consciously. If the stimulus is repeated at regular intervals, however, we habituate and so cease to notice it. E. R. John (1976) demonstrates that before habituation, electrical activity is widespread throughout the brain, suggesting that the information conveyed by the novel stimulus is widely available for multiple cognitive pathways. After habituation, however, event-related potentials can be found only in the stimulated sensory tract. This effect has been replicated: Dehane and Naccache (2001) presented words written backwards to subjects in two modes of presentation, one subliminal and one conscious. Those processed unconsciously produced high levels of activity in the word recognition areas of the cortex, while those processed consciously evoked much more widely distributed activity in the parietal and prefrontal cortex. These findings are consistent with the hypothesis that unconsciously processed stimuli are limited in their scope while the contents of conscious stimulation are globally accessible.

The impossibility of thought suppression, as demonstrated by Wegner (1989), provides a further example. Conscious expression of the desire not to think about something is almost

always self-defeating, and leads to the persistent recurrence of the thought to be suppressed (this is called 'ironic process theory'). For the brain to prevent thoughts from reaching the threshold of consciousness (and thereby being broadcast to pathways that might be undesirable, such as an emotion-processing pathway), it must *unconsciously* make the decision to repress those thoughts. The broadcast hypothesis explains this phenomenon: the conscious consideration of the thought to be repressed leads to its being broadcast, processed, and resurfacing in the conscious spotlight again.

According to the broadcast hypothesis, consciousness is an adaptation that integrates and distributes information in order to coordinate the activity of multiple specialized pathways within the brain. I have suggested several empirical phenomena in humans in which this is manifested; can the broadcast hypothesis also yield testable predictions for animal behavior?

CHAPTER 3

From the Theoretical to the Empirical: The Broadcast Hypothesis, Modularity, and Associative Learning

According to this view I advanced in the previous chapter, the information represented by a conscious mental state is made widely available for independent processors ('specialists,' following Baars' theater metaphor) throughout the brain. If this information were not broadcast globally, these specialist processors would not have reliable access to it, and so we expect that instances of conscious processing would have some observable effects distinct from unconscious processing. More specifically, we expect that these effects would involve interactions among the specialists, because the broadcasting of information takes a system of parallel processors that would otherwise be independent and automatic and coordinates their activity to produce a distributed but unified system.

In what follows, I press this thought further, with the goal of arriving at observable patterns of behavior that can be taken as proxy for consciousness. From there, reports of animal behavior across different taxa will furnish a substantive answer to the question of the distribution of consciousness in the animal kingdom. Thus, this chapter serves as a transition from a theoretical argument to an empirical one. I begin with a clarification of the metaphor invoked in the broadcast hypothesis. Global Workspace Theory turns on the notion that conscious states broadcast information in order to mobilize and coordinate a system of specialists – what are these specialists, and how does the broadcasting of information affect their performance?

3.1 Modularity

According to the theory of consciousness discussed in the preceding chapter, the brain is comprised by a number of theoretically dissociable 'specialists', or cognitive processors, which take a given input of information and compute some output. In Baars' metaphor, the brain was

like a theater filled with these specialists, each of which operates as an individual. Those in the audience are consciously impenetrable – their processing is never consciously experienced – although the outputs of their processing have direct bearing on the trajectory of the spotlight of attention.¹¹ Specialists onstage are consciously penetrable. Although the input and output of each specialist may be conscious or unconscious, information in the 'spotlight' of attention is theoretically visible by all the specialists, both onstage and off. In this way, the output of one specialist may become the input of any other specialist if it is broadcast.

I propose that we should understand the consciously impenetrable specialists as modules, which process information completely autonomously unless connected by the Global Workspace. Doing so allows us to bridge the gap between theoretical and experimental psychology. As such, I use this section to briefly discuss modularity and its relation to the Global Workspace. The topic has invited much debate over the past several decades, so I will remain neutral on those issues that are not immediately relevant to my purposes here.¹²

Fodor (1983) lists nine criteria of a module, and proposes that a system fits the definition if it has most of these “to some interesting extent.” Of these, the most essential are information encapsulation and limited central accessibility, which entail restriction on information flowing into and out of a module, respectively. This two-way restriction on information flow means that modules are self-contained. That is, they typically process information automatically and autonomously, without access to information stored in other modules.

In spite of this apparent rigidity, modules are not static in structure. In normal humans, the acquisition of new modules through experience is a commonplace occurrence. Any highly

11 As discussed in the previous chapter, the unconscious processing of information also bears heavily on the shaping of the contents of conscious experience (Baars, 2003).

12 For example, there is much disagreement about the extent to which the mind is modular (the 'massive' vs. 'modest' modularity debate) and to what extent modules are innate. For discussion and historical review of these and related topics, see Bechtel (2003).

practiced and automatic skill becomes unconscious, separate from other skills, and free from voluntary control – that is, modular (Posner and Snyder, 1975; Shiffrin and Schneider, 1977). Such processes of acquisition are typically guided by preexisting, inherited modules (Nesse and Lloyd, 1992).

3.2 GW Theory and Mobilization of Modules

Global Workspace Theory says that conscious states broadcast information to a system of specialists, including the modules I've just been describing. In so doing, consciousness provides the specialists with access to a 'global workspace' whereby they can coordinate their efforts: each specialist can process a given set of information simultaneously, and the results can be in turn sent back to the workspace to be broadcast to other specialists (or to the executive mechanisms that direct the 'spotlight' of attention).

By this coordination of specialists, consciousness takes the brain – otherwise a system of self-contained, parallel processors – and renders it a distributed, interconnected system. In an unconscious organism, each module acts on a limited amount of information, and its output is not accessible for other modules (information encapsulation and limited central accessibility). But if there is pervasive communication among these specialists, the system may perform more effectively, particularly in cases where the system is facing a problem without any clear precedent that must be handled adaptively. Global Workspace theory holds that this coordination of efforts takes place through conscious broadcasting of information, which enables access from any one component of the nervous system to all other components.

How does this manifest itself in behavior? Without conscious broadcasting, responses to stimuli are modular – that is, rigid and stereotyped. But if we posit mediating representations of information that are made accessible to a society of specialists through a Global Workspace, then

the same perceptual input can lead to divergent outputs and flexibility of behavior vis-a-vis intermodular communication.

This prediction aligns well with our knowledge of what sorts of everyday, real-life tasks necessitate conscious engagement. When we are confronted with a novel challenge, it takes deliberate, conscious processing in order to overcome it. (Consider the kinds of things that one cannot do if one is distracted: commit new facts to memory, read and understand an unfamiliar text, or learn a new skill, for instance). This conscious processing makes the contents of the task at hand available to all the specialists, in order to delegate the task of processing the information to whichever module or modules are best suited for it.¹³ Iteration of this process allows the entire system to coordinate the processing of many functionally distinct modules in new ways. If we perform the same task over and over (as we do when learning a new skill), we develop simpler means to reach the same end – we develop new modules, which often take components from preexisting components.

So, we would expect organisms with conscious mental processes to possess a certain adaptivity and plasticity of behavior that contrasts with the rigidity of those unconscious. This coheres with the common suggestion among cognitive ethologists that a high index of adaptivity is the most likely indicator of consciousness (Walker, 1983; Griffin, 1991, 2001; Allen and Bekoff, 1999). However, the evidence commonly cited in favor of such a proposition tends to be

13 The foundations of a scientific explanation for the phenomenal character of consciousness are in this thought. Conscious processes integrate information from many sources (including many sensory modalities) into a unified whole via the Global Workspace and broadcast that information to many modules. These modules are highly specialized and must be able to distinguish the information they can process from the information they cannot. Endowing conscious representations with a phenomenal component is one way of achieving this. One always experiences sounds *as sounds*, and information in that sensory modality is kept distinct from the information from other modalities with which it is consciously integrated in virtue of having a pitch, timbre, volume and so on. Making this sensory modality phenomenally different from others helps the brain distinguish auditory information, and varying the composite factors of the sound (pitch etc.) helps the brain distinguish among sounds. According to this view, subjective feel could be a natural consequence of a Global Workspace arrangement, wherein representational information integrated from many different sources must be kept distinct to be processed effectively.

anecdotal and rely heavily on our intuitions that such apparently sophisticated behavior couldn't occur in nature without some sort of consciously experienced thought process like the ones that we humans would use in problem-solving situations of comparable difficulty. In what follows, I suggest a basic form of adaptivity (flexible, non-operant associative learning) that has strong theoretical justification in Global Workspace theory as a litmus test for consciousness.

3.3 Adaptivity and Associative Learning

Adaptivity to one's environment and the problems there encountered takes many forms. While those that involve tool use or social deception (for example) involve a degree of sophistication that seems appropriate to consciously enabled behavior, at the other end of the spectrum are processes like habituation and sensitization, which have been experimentally demonstrated to occur in humans even in the absence of conscious awareness. Even the simplest animals show some degree of responsiveness to changes in their environment, and many instances of adaptivity might be explained by the gradual shaping of individual modules over time by means of neural plasticity, rather than intermodular communication or the mass modification of previously autonomic modules. We want to isolate behavioral patterns that are adaptive because they supervene on the efforts of multiple modules. We expect that these would be quick behavioral changes, as opposed to the gradual developmental changes enabled by synaptic plasticity.

Such adaptations may come in many forms, owing to the vast range of modular functions and of ways in which these functions may be enhanced through intermodular communication. One of the most universal and accessible forms of modular processing involves stimulus recognition. Schacter (1989) posits the existence of such "knowledge modules" (he gives a few example categories: conceptual, facial, spacial, or lexical recognition) as part of a model of

associative learning. According to Schacter's model, various knowledge modules interact through conscious recognition of the two stimuli to be associated. Connections among these modules are relegated to memory systems. Global Workspace theory explains the formation of these associations through consciousness thereof as an effect of their connection being broadcast to memory modules.

Accordingly, the typical experimental paradigm in humans used by advocates of Global Workspace Theory involves declarative memory (in particular, memory of word associations) (Baars, 1988; Squire, 1992; Clark et al., 2002; Cohen et al., 1997; Schacter, 1989). Novel word-combinations must be processed consciously in order to be retained, while routine ones can be processed subconsciously. The theoretical justification for such a process is that the global broadcasting of an association allows for a connection to be formed between disparate recognition modules. In the case of animals, of course, this suggestion is not applicable, as those animals with any form of rudimentary linguistic capabilities are those whose consciousness is least in question. Despite the difficulties of testing declarative memory in animals, however, we can examine a slightly broader phenomenon: that of non-operant associative learning.

For example, Clark and Squire (1998) demonstrate the role of declarative memory in associative learning by using a variant on a classical conditioning task. In an eyeblink-response test, subjects learn to associate a tone with an air puff blown in their eye. After several trials, a subject will blink automatically and reflexively in response to the tone. (That the association of the two stimuli is automatic rather than conscious is further evidenced by the fact that the same results are observed in amnesic human subjects, whose declarative memory is impaired). In trace conditioning, a variant of the the test, an interval (typically 500 to 1000 milliseconds) is inserted between the tone and and air puff. Clark and Squire found that the performance of human

subjects in the trace conditioning task varied, but there was a robust correlation between successfully acquiring the association and a conscious awareness of the association – which was unnecessary in the standard paradigm. Furthermore, amnesic patients (as well as animals with hippocampal lesions analogous to those of amnesic humans) failed altogether at the trace conditioning task.

These results suggest that trace conditioning of this form requires conscious attention, and, more broadly, that for an association to be acquired without conscious awareness it must fit within ecologically conditioned parameters. Animals that demonstrate flexibility in their associative capacities (for example, by succeeding not only at basic conditioning tasks but also those that involve time delays or disparate stimuli) are those that Global Workspace theory suggests are most likely to be conscious.

3.4 Associative Flexibility

Associative learning is fundamental to an organism's capacity to adjust to its environment. It is not surprising, therefore, that every animal that has been thoroughly tested has been shown to exhibit some associative behavioral pattern (Wynne, 2001). Gallistel (1993) suggests that this capability is so basic because events of significance to an animal typically occur at rates conditioned by other events in a time-dependent manner. Any animal that can respond to causality (apparent or actual) by forming cause-effect associations will have a clear predictive advantage over those that cannot. The universality of the most basic forms of associative learning may be the result of shared evolutionary history or a common adaptive response to the causal structure of nature.

Roitblat and von Fersen (1992) argue that the universality of associative learning allows for a “library” of essentially identical learning mechanisms across species. Macphail (1987)

makes the stronger claim that because associative learning is a 'building block' for higher-order cognitive functioning, there are essentially no differences in intelligence across nonhuman species: all animals have the same basic cognitive capacities, albeit to varying degrees. However, as the trace conditioning task demonstrates, the absence of conscious awareness can place limits on the capabilities of an organism's associative capacities. The kinds of associations that can be acquired without conscious awareness tend to be those that are simpler and more common in nature, involving ecologically stereotyped contingencies. Conscious awareness allows for a more flexible associative capacity, one that involves forming rapid connections between disparate stimuli.

So, my next step will be to survey associative learning capacities across different taxa. The diversity of ecological pressures on organisms and the ways in which those organisms adapt make it impossible to specify a single rigid criterion by which to distinguish conscious associations from unconscious ones, but I will operate on the premise that conscious associations are quicker and more flexible, whereas unconscious associations can only be formed using stimuli that are commonly connected in an organism's natural environment.

CHAPTER 4

Evidence of Associative Capacities and Consciousness Across the Animal Kingdom

Researchers from the nascent field of cognitive ethology have proposed several behavioral phenomena, including self-recognition, theory of mind, tool use, and communicative or social behavior, as potential indicators of consciousness (see Shettleworth, 1998 for review). Cognitive ethologists argue that such sophisticated patterns of activity involve higher-order thought and are unlikely to occur without primary consciousness. In the previous chapter, I advanced a different proposal: that consciousness would manifest itself in the flexibility and sophistication of an animal's associative capacities.¹⁴

The term 'associative learning' can be variously applied, and in its broadest sense it can be considered a near universal of animal behavior (Wynne, 2001). More specifically, it encompasses most basic adaptive learning (with the exceptions of habituation and sensitization) and consists in acquiring the ability to differentially respond to stimuli with predictive value. For example, almost all animals are sensitive to cues when they discover a high quality food source, and will subsequently use those cues in future foraging or hunting behavior. Associative capabilities, as I discuss in this chapter, reflect conspicuous, non-gradualistic variation across major animal taxa.

Global Workspace Theory implies, I have argued, that consciousness enables the rapid acquisition of non-stereotyped associations. The broadcasting of consciously processed information allows for disparate modules of cognitive processing (in this case, of stimulus recognition) to be brought together. So, we expect the associative capacities of animals with consciousness to be more rapid and flexible in nature, while animals without should at best be

¹⁴ In the survey of animal taxa that I undertake in this chapter, I include reports of such higher-order cognitive phenomena. These are supplementary to my argument, which hinges on associative learning capacities. I think it is no coincidence, however, that taxa with robust associative capacities also tend to show many of the more sophisticated behavioral patterns on which cognitive ethologists typically rely.

capable of acquiring associations resembling those that a member of their species would regularly encounter in its natural habitat.

In this chapter, I survey evidence of associative learning throughout the animal kingdom. I begin with the vertebrates, which I group according to the five major classes (mammals, birds, amphibians, reptiles, fish) and then turn to invertebrates, focusing on the most likely candidates based on observed cognitive complexity (honeybees and cephalopod molluscs). It is worth acknowledging the degree of oversimplification involved here. This imprecision is exacerbated by a biased pool of available evidence, given which animals have been studied and in what capacity. My generalizations depend on the assumption that the species that have been extensively studied are more or less representative of their kind.

Recognizing these limitations, I put forward the following substantive thesis about the status of animal consciousness:

- Primary consciousness is well-evidenced in mammals and birds.
- Reptiles, amphibians and fish may have some sort of dim consciousness or proto-consciousness, but the evidence is not convincing (perhaps owing in part to the paucity of scientific studies of reptile and amphibian cognition).
- There is little evidence that invertebrates are conscious, with the major exception of cephalopods.

This may be summarized by the conjecture that consciousness evolved independently at least twice (possibly a third time, in the case of cephalopods) after the divergence of the *anapsid* and *synapsid* reptilian lines that led to birds and mammals, respectively. Another possibility, however, is that subsequent research on creatures like amphibians and reptiles will show that they are, in fact, conscious in much the same way as birds and mammals, albeit with remarkably

weak memory – and that consciousness therefore evolved once in the vertebrate line.

4.1 Vertebrates

On neuroanatomical considerations, vertebrates have an obvious advantage over invertebrates in the search for consciousness. The hippocampus, which is essential for the functioning of declarative memory in humans, is present in all mammals (Baars, 2005). Its evolutionary predecessor and homologue, the pallium, is present in all vertebrates.

4.1.1 Mammals

For many mammals, scientific investigation is focused less on primary cognition and more on higher-order capacities, such as tool use, semantic communication, and theory of mind. Smith, Shields and Washburn (2003) suggest such forms of metacognition as the “royal road” to identifying animal consciousness. There are two major reasons for this kind of thinking. The first is the supposition that primary consciousness is evolutionarily prior to forms of higher-order awareness and cognition, and therefore that extreme ecological circumstances would be necessary to produce the latter in absence of the former. The second is the thought that higher-order cognition necessarily involves primary consciousness. There are two components to metacognition: an object-level mental process (such as a memory) and a meta-level, or executive, process that monitors the object-level process (Nelson and Narens, 1996). That the object-level mental process must be a conscious one is evidenced by the fact that impairment of declarative memory impedes performance on metacognitive tasks in humans (Nelson, 1996). Some, however, suggest that these processes could be implicit rather than declarative in animals (Proust, 2003; for summary of the current debate, see Smith et al., 2008). If one accepts metacognition as evidence for consciousness, then there can be little doubt about the consciousness of many primate and cetacean species, and subsequent research on other mammals

may also show them to succeed at similar tasks (Smith et al., 2003).

Metacognitive evidence aside, there is strong evidence for mammalian consciousness based on the flexibility of their associative capacities. While there is, of course, variation across species, mammals (including those less commonly studied in labs, such as farm animals) can generally form associations with arbitrary stimuli, including those unencountered in their natural habitat (Rogers and Kaplan, 2004). Even marsupials, which are sometimes assumed to be cognitively inferior to placental mammals, excel at forming quick associations with novel stimuli (Wynne and McLean, 1999). More impressively, those mammals thus far tested with trace eyeblink conditioning (mice, rats and rabbits) were all capable of acquiring the association – which necessitates a functional declarative memory in humans (Takehara et al., 2002; Weiss et al., 1999; Powell and Churchwell, 2002). As in the case of humans, hippocampal lesions undermine performance.

Given their higher-order cognitive capacities, evolutionary continuity, neuroanatomic similarity, and – above all – robust associative learning skills, there is strong evidence that consciousness is common to mammals. Owing to the dangers of anthropomorphism, scientists tend to resist mentalistic language when describing animal behavior, but it is near certain that perception and cognition in other mammals, as in humans, is at least partially conscious and experienced.

4.1.2 Birds

There is more room for doubt in the case of birds because of the larger evolutionary gap that separates us from them. Birds and mammals descended from different evolutionary branches of reptiles, the anapsids (these include most modern day reptiles) and the synapsids (the immediate reptile precursors of mammals) respectively, about 300 million years ago (Kardong,

1995). Although evolutionary continuity starts to lose its argumentative force here, the behavioral evidence for avian consciousness is extensive and has received much attention from cognitive ethologists in recent years.

In particular, the avian capacity for metacognition has been taking as telling evidence, although as in the case of mammals, the connection between higher-order cognition and primary consciousness is disputed. If we accept metacognitive capacities as proxy for consciousness, then there can be little doubt about the status of many species of birds (Edelman et al., 2005). Even commonplace birds like pigeons seem to be capable of higher-order discrimination tasks; Zentall et al. (2001) for instance conducted an experiment in which they first taught pigeons to respond to one stimulus by pecking it and another by refraining from pecking. Once the pigeons had learned this rule, the experimenters added a second round to each trial in which they had the choice of pecking a red or a green region, where red was the correct answer if they had just pecked and green was the correct answer if they had refrained from pecking. The pigeons were capable of learning this discrimination, which seems to reflect the capacity to recall one's own behavior. The metacognitive status of these results is contested, however: while Zentall et al. take this to be indicative of episodic memory, another interpretation suggests that this is rather a case of operant conditioning, in which the animal's response in the first part of the experiment serves as the unconditioned stimulus in the second part. The rudimentary linguistic capacities of certain other birds, however, makes for simpler identification of metacognition. Pepperberg (2006) trained Alex, an African Grey parrot to understand and verbally identify not just simple qualities like red or blue, but also higher-order concepts like same/different. Alex performed equally well on these tasks with novel and familiar objects and was also able to identify *what* was the same or different (either “color” “shape” or “mah-mah,” which is Alex's word for

'material'). There is also evidence that many species of birds also possess a theory of mind, the ability to appreciate the mental states (e.g. desires, false beliefs) of other individuals. Since recognition of the mental states of another seems improbable if an individual does not experience similar mental states, theory of mind seems like a metacognitive process that would be highly unlikely to evolve without primary consciousness. Birds appear to use theory of mind most commonly in order to thwart enemies: bee-eaters modify their behavior on consideration of what a predator can or cannot see (Watve et al., 2002); food-caching ravens show more hostility towards competitors who observed where they cached (Bugnyar and Heinrich, 2005); plovers feign an injury in order to distract predators from their nests (Ristau, 1991).

Of course, there remains the possibility that any higher-order cognitive tasks could be implicit rather than declarative – and that therefore they are no indicator of primary consciousness (Proust, 2003). Nonetheless, many of the aforementioned discrimination tasks necessitate first learning basic associations, and birds excel at this, showing a level of flexibility indicative of conscious broadcasting. It has long been known that pigeons are capable of learning complex associations with neutral, arbitrary associations such as color samples or lines of varying orientation (Carter and Eckerman, 1975). Indeed, while mammals tend to outperform birds on metacognitive tasks, they are near rivals when it comes to first-order associative capacities in terms of the speed at which they acquire associations (Rogers and Kaplan, 2004). Further supporting the parallel between avian and mammal capabilities, the critical structures assumed to be necessary for consciousness in mammalian brains (i.e., the thalamocortical system) have their homologous counterparts in avian brains (Butler et al., 2005; Jarvis et al. 2005). Reilly and Good (1989), furthermore, found that lesions to these areas in pigeons impaired associative learning in a fashion similar to that observed in mammals.

4.1.3 Reptiles, Amphibians and Fishes

Species in these classes exhibit none of the aforementioned metacognitive phenomena. Fishes, however, have long been known to be capable of social learning (Helfman and Schultz, 1984; see Brown and Laland, 2003 for review), and so their cognitive capacities have been extensively studied. In contrast, reptiles and amphibians were previously believed to be incapable of simple learning altogether (Hodos and Campbell, 1969; Burghardt, 1977), and so their basic cognition has received little scientific attention. Thomson and Boice (1975), for example, showed that frogs failed at one of the most common operant conditioning paradigms of the time, in which subjects learn to associate predictive stimuli (such as a coterminal tone, or the appearance of the testing chamber) with an electric shock. Recent research shows, however, that species in all of these classes are capable of associative learning, albeit in a vary narrow sense of the term.

For instance, Woody and Mathis (1998) tested that ability of newts to associate chemical signals from a novel predator with another chemical stimulus. Newts were successful when the second stimulus was the skin extract of a conspecific (a familiar fright stimulus, Woody and Mathis point out). Newts failed to acquire associations with the skin extract of terrestrial salamanders or a neutral stimulus (distilled water). Most other instances of associative learning in reptiles and amphibians have this general structure, in which the “releasing valence” of one stimulus is transferred to another (Suboski, 1992). For instance, toads selectively approach and direct feeding responses to odor stimuli from prey that they have previously ingested in preference to odors from novel prey (Dole, Rose and Tachiki, 1981). Examples of associative behavior in reptiles are similarly structured (Powers, 1990). There is evidence that reptiles outperform amphibians when it comes to taste aversion acquisition, but in general the cognitive

differences between the two classes are not pronounced (Paradis and Cabanac, 2004).

Suboski (1992) argues that such cases are not clear examples of instrumental conditioning. He characterizes the associations these taxa are capable of making as a “releasing-stimulus-induced redirection of innately organized released responses.” When reptile or amphibian is presented with a neutral stimulus that it might naturally encounter in conjunction with a conditioned stimulus (e.g. a given scent with a certain food), it learns to associate the two stimuli in Pavlovian fashion. In short, experience enables them to learn which stimuli to respond to rather than how to respond to a particular stimulus.

The case for fishes is quite similar. As Kieffer and Colgain (2004) point out, most non-imitative behavioral changes in fishes can be explained as innate patterns of maturation, imprinting or basic trial-and-error learning. In general, they fail at associative learning tasks, although Brown et al. (2006) discuss many cases in which – similar to the newts of Woody and Mathis (1998) – fish learn to avoid a new stimulus through its association with a familiar fright stimulus. They classify this ability as releaser-induced recognition learning, following Suboski (1992).

Fishes, amphibians and reptiles are unable to form flexible associations involving arbitrary stimuli, and they also perform drastically worse than mammals or birds in operant conditioning tasks. This evidence does not support the claim that animals of these classes are conscious. The rift between mammals and birds on the one hand, and reptiles, amphibians and fishes on the other is not surprising when their brain-to-body-mass ratio is taken into consideration. Jerison and Barlow (1985) compiled the ratios for about fifty species of each class and plotted them on a graph of brain mass versus body mass, and found that results fell into two roughly linear clusters. The linear cluster representing mammals and birds had a greater slope

(representing a tendency to have a higher brain-to-body-mass ratio) and was higher on the vertical axis (representing a tendency to have a larger brain mass for the same body mass) than the linear cluster representing reptiles, fishes and amphibians.

For reasons discussed in chapter 1, however, we might assume that the cognitive aspects of consciousness are evolutionarily subsequent to its phenomenal aspects – and that therefore these taxa could experience some form of proto-consciousness. This, presumably, which would be predominantly phenomenal (though perhaps 'dimmer' in its phenomenal content) and minimally cognitive, with perhaps selectively fewer stimuli forming 'blips on the radar' of consciousness and impoverished memory. Such circumstance would account for poor performance on associative learning tasks in spite of some sort of subjective experience. It may also be that such proto-consciousness is common to some, but not all, of these animals, despite the similarity of cognitive style and their overlap in brain-to-body-mass ratio. For the time being I leave this question open, returning to the question of sentience in non-mammalian, non-avian vertebrates in closing.

4.2 Invertebrates

Given that only two of the five major classes of vertebrates show convincing evidence of consciousness, it seems improbable that we will find it in taxa even farther removed from us on the phylogenetic tree. Anatomical considerations make the prospects look even dimmer: while invertebrates are similar to vertebrates at the local level (i.e. process of conduction and synaptic transmission) they differ dramatically at the global level (i.e. cell structure, dendritic elaboration, and organizational structure) (Bullock and Horridge, 1965, Roitblat and von Fersen, 1992).

According to Global Workspace Theory, consciousness is not so much a localized process of the brain but rather involves global communication and coordination of its constituent modules – so

the global differences in structure between vertebrate and invertebrate neuroanatomy suggest that we should press skepticism about claims of apparent invertebrate consciousness.

Generally speaking, the evidence for associative capacities in invertebrates are weak. Carew and Sahley (1986) survey evidence in a number of species including bees, slugs, sea slugs, pond snails, land snails, leeches, locusts, and fruit flies, and conclude that in all cases, putative examples of learning “can be localized to individual neurons and involve alterations of either previously existing synaptic connections or intrinsic cellular properties; in no case have novel synaptic connections or new biophysical properties been induced by learning. The tentative principle then appears to be that certain neurons or groups of neurons are endowed with the capacity for plastic change, and experience then promotes that change in previously existing circuits.”

Nonetheless, invertebrates are incredibly diverse (with about a million species accounting for 95% of all animal species) and there have been proposed exceptions to the general rule that invertebrates are unconscious. Notably, cephalopods have been shown to be capable of remarkably complex cognitive tasks, and are generally understood to surpass many lower vertebrates in their intelligence (e.g. Mather, 2008). The other invertebrate with sufficient behavioral sophistication to attract the attention of cognitive ethologists is the honeybee (e.g. Griffin, 2001). Here, I examine putative cases of conscious behavior in bees so as to defend the general claim that invertebrates are not conscious, and conclude by examining cephalopods as an intriguing probable exception that requires further study.

4.2.1 Bees

Honeybees are sensitive to environmental clues about profitability of food sources, and learn to associate food sources with both visual and olfactory stimuli, with a higher sensitivity to

the latter (Carew and Sahley, 1986). Bitterman (1996) reviews a series of experiments designed to test the interaction of stimuli in these two modalities. He points out that many phenomena of associative learning with compound stimuli that are commonly observed in vertebrates are also observed in honeybees, but only if the composite stimuli are of the same sensory modality.

One such phenomenon is overshadowing, in which conditioning to a compound stimulus (e.g. red square and blue circle together) results in a weaker conditioning to each of the composite stimuli than would be acquired through individual conditioning (first the red square, and then separately the blue circle). This effect was only observed in honeybees when both stimuli were within the same sensory modality. That is, in the case of intermodal stimulus compounds (color-odor, dot-odor), the valence of one stimulus did not overshadow the valence of the other: the strength of the compound stimulus was the sum of the strength of each stimulus when tested individually.

Along the same lines, Funayama, Couvillon and Bitterman (1995) found that honeybees do not exhibit cross-modal blocking. In the phenomenon of blocking, the subject is conditioned to one stimulus (red square) and then a compound stimulus including the original stimulus (red square and blue circle together). Following this, the subject is conditioned to the second individual stimulus (blue circle) more weakly than if it had been presented by itself or in compound with an unconditioned stimulus: the conditioning of the first stimulus 'blocks' the strength of the conditioning of the second. Blocking occurred only when the stimuli were of the same modality.

These findings are consistent with Gould's (1996) proposal that bees have a separate 'slot' in memory for each feature a flower is likely to have. It is as if the processing pathways that associate cues of a given sensory modality with reward were modular – that is, self-contained

and autonomic, rather than integrated in an intermodal representation. As Allen-Hermanson (2008) suggests, rather than responding to conscious representations of their environment, they may instead be responding to fragmentary stimulus point-sources.

So, although honeybees are capable of associative learning to a remarkable degree of sophistication, information from multiple modalities is kept separate, suggesting that honeybee cognition lacks the integrative structure or flexibility of access that is evidential of consciousness. Their associative capacities appear to be ecologically stereotyped, which is not surprising given their ecological niche as eusocial animals, with specialized foragers that must adapt to fast and unpredictable changes in the availability of food (and are, furthermore, undistracted by other activities like mating and nest construction).

4.2.2 Cephalopods

Many species of cephalopods have been found to rival higher vertebrates in terms of neuroanatomical complexity. The nervous system of cephalopods is unlike anything else documented in invertebrates. Going by number of neurons alone, they are comparable to most vertebrates: octopuses, for instance, have 170 million brain cells¹⁵ (the vast majority of which are neurons), putting them on near-equal footing with the average dog (Giuditta et al., 1970). Normalized to body mass, their relative brain size exceeds that of many lower vertebrates, sometimes approaching that of birds (Hanlon and Messenger, 2002). Neurocomplexity, however, can only go so far: since cephalopod nervous systems differ so drastically from vertebrate nervous systems at the global level, it is unclear where, structurally, scientists should look for the potential correlates of consciousness. There are no clear analogies, for example, to the re-entrant

¹⁵ Interestingly, this only constitutes about 1/3 of the total octopus nervous system; the other 2/3 is distributed through the arms (Giuditta et al., 1970). If consciousness is present in these animals, it doubtlessly involves a very foreign form of embodiment from what we are accustomed to.

loops in the mammalian thalamocortical system (Edelman et al., 2005).¹⁶

The complex behavioral repertoire of cephalopods is the second major reason to believe there might be something going on in terms of consciousness. Patterns of behavior are domain-general and can be adopted in a range of circumstances, as in the use of propulsive water jets to build shelters, repel fish, or manipulate objects (Mather, 2008). They are ready learners, prone to explore new environments and to acclimate to novel objects by playing with them (Kuba et al., 2006; Mather and Anderson, 1999). There are also reports of tool use. Mather (2009) suggested the modification of homes by rearranging rocks and debris as a potential instance; and some octopuses have been documented carrying coconut shells with them as they skim the ocean floor and withdrawing into the shell for protection (Finn et al., 2009). They excel at basic learning tasks; current focus is to see whether they are capable of higher-order cognitive tasks. Hvorecny et al. (2007), for instance, found evidence of conditional discrimination. In this experiment, octopuses and cuttlefish were trained to find their way out of two structurally similar mazes with different escape routes. After training was complete, the subjects were put in either maze in randomized order. Using visual information, they were able to recall which maze was which, and approach the correct exit directly rather than by trial and error. More remarkably, Fiorito and Scotto (1992) report a case of observational learning, which, if confirmed, would be remarkable – most mammals fail at such tasks. As these reports have not been replicated, however, there is controversy as to whether Fiorito and Scotto's observations could have an alternative explanation.

While evidence of higher-order cognition is contested, however, the associative capacities of cephalopods has long been known to exceed that of other invertebrates (Hanlon and Messenger, 2002). They are capable of learning associative stimuli either simultaneously or

¹⁶ For a review of cephalopod neuroanatomy, see Hochner et al. (2006).

successively and can learn multiple associations at once (Messenger, 1977). The associations they are capable of making show considerable flexibility, moreover. They can make visual and tactile discriminations, and can learn to selectively attack or refrain from attacking stimuli for positive reinforcement (typically food) or negative reinforcement (e.g. electric shock). Although performance on such tests can be erratic,¹⁷ associations, when successfully acquired, are acquired rapidly (Papini and Bitterman, 1991; Darmaillacq et al., 2003). They are capable of acting against their natural inclinations on the basis of learned associations. For instance, although octopuses reliably avoid well-lit areas, Maldonado (1968, 1969) trained octopuses to leave a dark box for the light to avoid electric shock. Moreover, cephalopods are highly sensitive to a range of visual stimuli, and are able to discriminate an original figure from a mirror image or a 90 degree rotation that shared the same vertical and horizontal extents (Sutherland, 1963).

This evidence in favor of cephalopod consciousness is robust. This provides a remarkable example of convergent evolution of the nervous system: the most recent common ancestor shared by mammals, birds and cephalopods lived over 600 million years ago, before the Cambrian explosion. Further experimentation may help us to gain a better appreciation of the ways on which they are conscious – Mather (2008) takes the ease with which they switch between visual and non-visual guidance when manipulating objects like clams to suggest some rudimentary body image or sense of self.¹⁸

4.3 Summary

Mammals, birds and cephalopods are all capable of adapting to their environment – as

¹⁷ Cephalopod trainers sometimes muse that this sort of performance might be explained by subjects being too smart rather than too stupid: knowing that they will be fed anyway, they opt not to comply with the experiment.

¹⁸ Roy Caldwell, a specialist in stomatopod crustaceans at the University of California-Berkeley, has informally suggested another marine invertebrate as a possible rival of cephalopods in terms of cognitive complexity: the mantis shrimp. For discussion, see: <<http://www.blueboard.com/mantis/logs/020507.htm>>.

well as to novel stimuli – through flexible associative learning, which suggests a global broadcasting of connections among stimulus recognition modules. Unsurprisingly, these taxa include species with behavioral patterns suggestive of higher-order thought, while lower taxa are at best able to perform associative learning tasks within ecologically stereotyped conditions through releaser-induced recognition. Of these lower taxa, reptiles, amphibians and fish – the remaining vertebrates, and evolutionary predecessors of birds and mammals – seem possible candidates for some phenomenal proto-consciousness that operates without a strong sense of memory. Though honeybees outperform these classes on such associative tasks, there is much more room for doubt in their case, for several reasons: (1) they do not share evolutionary continuity with definitively conscious species, as reptiles, amphibians and fish do; (2) their global neuroanatomical structure is radically different from that of conscious animals; (3) their associative capacities appear to function within separate modalities, while conscious processing involves the integration of modal information. Although the first two of these reasons are also applicable to cephalopods, the associative capacities of honeybees is easily explained without positing consciousness, as the result of evolutionary pressures on a eusocial species whose foragers must be sensitive to context clues regarding food sources if the hive is to subsist. Cephalopods, by contrast, are typically solitary creatures, and – like mammals and birds – they are sensitive to stimuli they would not normally encounter and also appear to be capable of more advanced cognitive processes such as tool use.

I conclude, therefore, that mammals, birds, cephalopods are conscious in a way that bears cognitive similarity to our own consciousness. Furthermore, along with (potentially) reptiles, amphibians and fish, these creatures are capable of phenomenal experience – capable of, for example, experiencing pain. How should this inform the way we coexist with these animals?

CHAPTER 5 Animal Consciousness and Ethics

There has been a revival in interest in animal rights in recent years, particularly among philosophers. Following Singer (1975), these thinkers challenge the view that the interests of humans are categorically different, or somehow more worthy of ethical consideration, than those of animals (“speciesism”). There is little consensus among proponents of this view about how best to reconcile conflicts of human and animal interest or what degree of moral status is appropriate, though most agree that, if animals should have rights at all, it is first in virtue of their being phenomenally conscious beings – beings who are capable of experiencing pleasure, pain, desires, and so on. As Bentham (1823) famously put it, “the question is not, Can they *reason?* nor, Can they *talk?* but, Can they *suffer?*”

Extending moral status to animals means including them in our moral policy – not as agents eligible for moral responsibility, but as patients to whom we moral agents can properly have responsibilities and obligations. So, although we might argue that chimpanzees have the right to live, this doesn't mean that their natural predators are morally culpable or that we should try to intervene. It means only that we should modify our own conduct so that we do not violate their natural interests, and that violation of those interests constitutes moral wrong.

In particular, it means that we should take their interests *qua* individuals into account. Sometimes we act for the good of a species, like when we implement policy protecting those in danger of extinction. It would seem that in such cases our reasons are predominantly ecological: we are trying to minimize the extent of our destructive impact upon nature. Whether we also have moral grounds to protect species is an entirely different question that, as Korsgaard (forthcoming) points out, inherits many practical difficulties when one considers how to deal

with issues where one's species interests must be sacrificed if another is to be saved.

In this chapter, I examine the connection between consciousness and moral status. Do theories about the distribution of consciousness in the animal kingdom (such as the one I have proposed) bring us any closer to resolution of substantive ethical questions? In particular, I discuss whether phenomenal experience should constitute a necessary and sufficient condition for moral consideration and the moral relevance of different ways an organism can be conscious.¹⁹

5.1 Is Phenomenal Experience Necessary?

There's a strong intuitive connection between being capable of phenomenal experience and possession of moral status. It is plainly permissible to kill and eat a plant or to get angry at a computer (although we share certain qualities with plants and computers – namely life and sophisticated cognitive capacities – that may have appear to have moral import). After all, these entities are not capable of experiencing the pain or indignation that these activities might provoke in a conscious being. A perennial plant may have an interest in prolonging its own life, and, if left undisturbed, will reliably behave in pursuit of this interest. But a plant cannot know *what it is like* to have one's interests violated or ignored. And it is this experiential capacity that seems to justify our most basic claims to moral considerability: I object to pain, for instance, because I know what pain feels like and know that I have an interest in avoiding it. So I take our intuitions that some degree of phenomenal experience is a necessary condition of moral status to be well-founded.²⁰ Many entities have interests in a broad sense of the word, but those interests merit our ethical attention when there is, at least minimally, 'somebody home' to consciously

19 More precisely: different mental processes that an organism is capable of consciously experiencing.

20 For a dissenting view, see Vergood and Visser, 1997.

experience those interests or the adverse consequences of their frustration.

Of course, we can still have moral obligations involving phenomenally unaware entities. One could argue, for example, that there are moral reasons to be respectful of nature. But although this means I shouldn't purposelessly destroy a forest – even one devoid of fauna – the obligation here is not owed to the forest itself but to the conscious beings to whom the forest (or, more generally, nature) matters.

Having phenomenal experience entails, at least potentially, being the kind of entity to whom moral obligations can be directly owed. Next, I ask: what else besides subjective experience is relevant?

5.2 Is Phenomenal Experience Sufficient?

I mentioned above that when we object to something, it is first in virtue of our capacity to consciously experience the effects of the action in question. My ability to experience pain licenses my objection to others causing me to suffer (indeed, it wouldn't make sense to call my plight suffering if I did not experience it). But there are other ways in which one's interests can be violated – other ways in which one can be morally wronged. When I object to a moral wrong, I am often objecting to more than just the immediate undesired consequences. For example, I might object on the grounds that my adherence to some sort of social contract has not been reciprocated, like when someone fails to uphold their end of a promise. Grounds for moral indignation of this particular kind are not applicable to the case of animals: since they cannot be agents in our moral system they cannot enter into moral agreements the way that we can.

There are, however, further reasons for moral objection that are more closely linked to patiency. As I previously mentioned, when someone victimizes me, it might be that my

immediate interests are jeopardized (like in the case of pain). In other cases it is future interests that are infringed upon, like when some case of harm renders the victim incapacitated. Or, sometimes we object to an action irrespective of its consequences, because it constitutes a violation of dignity. Underlying this notion is the thought that I am a person; I take myself to have worth (and, therefore, my interests *matter*) and I expect others to recognize that worth and to treat me accordingly. I take the cognitive apparatus underlying the capacity to object on these grounds in the first case to be some form of persisting memory and in the second case to be some basic sense of selfhood.²¹

I have argued in favor of the general intuition that an entity's interests are eligible for moral considerability if that entity has some form of conscious experience. But there are many mental processes an organism may be capable of experiencing, some of them more 'basic' than others (e.g. a consciously experienced sensory representation of the environment is presumably more 'basic' than a consciously experienced attitude towards a particular feature of that environment). Organisms with weak memory and an evolutionarily basic phenomenal capacity ('proto-consciousness') may only be capable of experiencing the 'here-and-now.' Such a creature may experience in any one moment the thwarting of its interests for the present and for the near

21 I resist the term "self-consciousness" here because I think the current paradigms for measuring what scientists call self-consciousness are still too rigid to capture what I am talking about here. The current scientific paradigm is the red dot test: an animal is allowed to acclimate to a mirror so as to gain an understanding of its own physicality. Then, while the animal is under sedation, experimenters paint a red dot on the animal's forehead. If the next time the animal views itself in the mirror, it reacts to the red dot, it can be said to possess a sense of self. This test is problematic in that it is too strict. Certainly, an awareness of a change in one's physicality evinces a sense of self, but the failure of some species to pass the test could be explained by a multitude of other factors (Bekoff, 2003). Many species do not naturally make self-directed movement toward their head (gorillas, for example, tend to avoid eye contact). Other species may recognize the change but be indifferent to it, perhaps because they are accustomed to getting food on their faces or to seeing food stains on the faces of conspecifics (Pepperberg et al., 1995). Furthermore, the experiment operates within a strictly visual paradigm, although it is also possible that some animals have a sense of self that relies more heavily on other modalities (it is well known, for instance, that a great deal of social interaction among dogs is done using olfactory cues).

future, but it cannot have a full appreciation of its future possibilities, cannot consciously form plans that could be infringed upon. Nor can it, as it were, reflect on previous transgressions, and in so doing prolong conscious experiences that may involve resentment or indignation. To put the same point another way: a stronger memory allows for otherwise fragmentary conscious experience to be connected so that an animal could consciously appreciate temporality. Animals with this capacity could have conscious experiences not just of immediate perceptions and desires but also of expectations, hopes, and recollection of the past (with all the emotional baggage entailed). I speculate that a robust memory is a necessary precondition for creating a sense of self in organisms. Blanke and Metzinger (2008) suggest that embodiment, which involves the conscious experience of a body as a unified whole, is essential to create what they call “minimal phenomenal selfhood,” and it seems probable that higher-order thought would conduce to this capacity. Appreciating one's self as an agent, as the holder of one's desires and the one made to suffer in a moral transgression allows an organism to consciously experience its investment in its interests.

The degree to which a being is conscious – of its immediate sensations, of its future and past, of its self, and so on – seems to have a genuine bearing on the ways that being's interests can be violated. How to interpret this result?

Many thinkers have proposed a cut-off criterion for moral status. Some, like Singer, draw the line at phenomenal experience, arguing that if a being is capable of suffering at all, its interests should merit our attention. Others take some form of higher-order thought or sense of self to be essential for moral considerability. Wise (2002), for example, proposes the relevant criterion to be 'practical autonomy,' which includes the capacity to intentionally try to fulfill

one's desires and possess a sense of self-sufficiency to enable a dim understanding of one's self as the being who wants something and is trying to get it. He remarks that (phenomenal) consciousness, though not necessarily self-consciousness, is implicit in the notion of practical autonomy. Along similar lines, Regan (1983) suggests moral status should be accorded to those beings who can rightly be called the "subject-of-a-life." To qualify, an organism must experience beliefs, desires, emotions, have a sense of the future, and the ability to initiate action in pursuit of desires and goals. Regan suggests that all mammals of at least one year old easily fit this description.

I agree with these thinkers that the degree to which a being can be said to be conscious (or, more precisely, what sorts of mental processes an organism is capable of experiencing) should not be taken lightly. There is something immediately more tragic about the unnecessary death of an organism who can appreciate its life to a fuller degree than about the death of a less aware organism. I think, however, that theories that propose an all-or-nothing criterion for moral standing rely on an oversimplified understanding of consciousness. Consciousness varies conspicuously in degree through the animal kingdom and any moral system centered around consciousness should take that into account. There are a number of ways to do this; I here propose two possibilities.

One reading of the gradation of consciousness might also construe moral status as a graded variable. According to this view, if you have a more sophisticated consciousness, you have higher moral status – your interests matter more. Pursuing this train of thought, we could structure a rough moral hierarchy following the different levels of consciousness I previously

suggested: primary phenomenal experience, awareness of the past and future, a sense of self.²²

The specifics of this view are open to interpretation: perhaps possession of a sense of self means one's interests are nearly incommensurate with those of humans, or perhaps it only puts one a small step above conscious animals with an appreciation of the future and past. In any case, this line of thought is especially conducive to attempts to vindicate current practice involving human parasitism on animals (e.g. use of labrats) because it justifies putting our own interests on a higher ground.

Another, more deontological way to approach the gradation of consciousness might first involve according equal moral status to all conscious animals. If an animal is capable of experiencing pain, pleasure and the like, then its interests are just as worthy of our consideration as any other such sentient creature. Different degrees of consciousness come into play because they have bearing on what sort of interests an animal is capable of having: while the interests of an organism with a sense of selfhood differ substantively from those of an organism with a more rudimentary consciousness, the difference lies in the type, not weight, of the interests. While all conscious organisms have basic interests in the essentials of survival, certain higher animals are also capable of having, for instance, emotional or socially-derived wants and needs that we are obliged to recognize.

5.3 Conclusion

Ethically speaking, what is the bottom line of the argument about the distribution of consciousness that I've advanced? There are two important points to be made. The first has to do

²² Though of course others could be proposed, perhaps with greater precision – ideally, the study of consciousness in the animal kingdom will advance and we will come to better understand how it varies and what mechanisms enable that variation.

with our treatment of those animals that we do not take to be in any way phenomenally aware (according to my argument, this consists of the non-cephalopod invertebrates). Are we free to treat these animals as mere means, on equal par with, say, lettuce? In an important sense, yes: if we cannot morally owe anything to these creatures, cannot do them wrong no matter how we treat them, then we should feel no guilt when we step on a cockroach. In some cases, it might even be prudent to make use of what some of these creatures have to offer – in an ideal world, perhaps we could cut back on the slaughter of mammals and birds by harvesting cognitively simpler edible organisms like crabs and lobsters, for example. I don't think, however, their lack of phenomenal awareness necessarily licenses acting towards them in purposelessly destructive ways. Even if pouring salt on a slug is, as it were, of no loss to the slug, there's a sense in which it still seems objectionable or inhumane. Kant famously thought that although we could not owe duties directly to any animal, we still owed it to ourselves not to use or mistreat them without reason. Wanton cruelty stifles our own humanity, and when we act in such ways we fail to cultivate empathy and benevolence in ourselves. While I don't think we necessarily have a self-owed moral obligation in the way Kant does, I do think there's something to be said for the cultivation of humane values and of respect for nature. It's one thing to remove a wasp's nest from one's home; it's another to go jumping on anthills for sport.

The second point is that consciousness is difficult to simplify, and if we're being completely honest about our ethical practice we need to deepen our understanding of the way consciousness varies and of its evolutionary history. If we can begin to classify the sorts of mental processes that different taxa consciously experience (the immediate perceptual present, a sense of selfhood, etc.) we will have a better appreciation of what sorts of interests species of

those taxa could hold – and how we could reasonably accommodate them.

Ideally, we will eventually be able to trace the evolution of consciousness backwards, and ultimately discover what sort of experiences might be the first ones to 'rise to the surface.' One highly feasible (and ethically loaded) answer is pain, as the detection of noxious stimuli carries with it an urgency that would be well-served by conscious broadcasting to multiple response systems. If this is the case, then perhaps it's all the more important to interpret findings about animal consciousness charitably – and to assume some ethically relevant phenomenal experience where it seems possible. Within the context of my argument, this would include reptiles, amphibians, and fishes. One major scientific paradigm that seeks to identify pain involves application of noxious stimulus both in control conditions and under analgesia (Bateson, 1991). An animal is concluded to undergo the experience of pain, rather than just the physical process of nociception, if the behaviors it displays in response to the noxious stimulus are not reflexive or stereotyped, and if these behaviors abate under anesthesia. While, as Rutherford (2002) points out, the interpretation of such experiments is disputed (and often clouded by hidden agendas), fishes, reptiles and amphibians have all been observed to demonstrate the aforementioned behavioral responses to noxious stimulus and to anesthesia (Sneddon, 2003; Machin, 1999; Bennett, 1991). The case for pain in non-cephalopod invertebrates according to this paradigm is much weaker, with the tentative exception of certain decapod crustaceans (Barr et al., 2007).

The bottom line, then, is that when it comes to animal consciousness, much still remains to be clarified. Besides trying to unearth patterns of consciousness' evolution so as to better understand the variation in the mental lives of other animals, another worthwhile direction for cognitive ethology might involve modifying (or vindicating) the scientific paradigms for pain

measurement and studying the nociceptive behaviors and analgesic responses of more animals, especially invertebrates.

(15,939 words)

References

Chapter 1

- Blackmore, Susan (2006). *Conversations on Consciousness*. Oxford: Oxford University Press.
- Block, Ned (1996). "On a Confusion About a Function of Consciousness." *The Behavioral and Brain Sciences* 18(2): 227-247.
- Chalmers, David (1996). *The Conscious Mind: In Search of a Fundamental Theory*. Oxford: Oxford University Press.
- Churchland, Patricia (2002). *Brain-wise: Studies in Neurophilosophy*. Cambridge: The MIT Press.
- Crick, Francis and Koch, Christopher (1998). "Consciousness and Neuroscience." *Cerebral Cortex* 8: 97-107.
- Dennett, Daniel (1995). "Animal Consciousness: What Matters and Why?" *Social Research* 62: 691-710.
- Edelman, Gerald (2003). "Naturalizing Consciousness: A Theoretical Framework." *Proceedings of the National Academy of Sciences of the United States of America* 100: 5520-24.
- Ellis, Ralph and Newton, Natika (1998). "Three Paradoxes of Phenomenal Consciousness: Bridging the Explanatory Gap." *Journal of Consciousness Studies* 5: 419-442.
- Emmerton, Jacky; Lohmann, Anette; and Niemann, Joachim (1997). "Pigeons' Serial Ordering of Numerosity with Visual Arrays." *Animal Learning and Behavior* 25(2): 234-244.
- Gray, Heather; Gray, Kurt and Wegner, Daniel (2007). "Dimensions of Mind Perception." *Science*, 315(5812): 619.
- Griffin, Donald (1984). *Animal Thinking*. Cambridge: Harvard University Press.
- Griffin, Donald (2001). *Animal Minds: Beyond Cognition to Consciousness*. Chicago: University of Chicago Press.
- Kihlstrom, John (1987). "The Cognitive Unconscious." *Science* 237: 1445-1452.
- Mandler, George (2003). "Consciousness: Respectable, Useful, and Probably Necessary." In Baars, Bernard; Banks, William; and Newman, James (eds.), *Essential Sources in the Scientific Study of Consciousness*. Cambridge: MIT Press.

Nagel, Thomas (1974). "What Is It Like to Be a Bat?" *Philosophical Review* 83: 435-450.

Nagel, Thomas (1986). *The View from Nowhere*. Oxford: Oxford University Press.

Pepperberg, Irene (2006). "Ordinality and Inferential Abilities of a Grey Parrot (*Psittacus erithacus*)." *Journal of Comparative Psychology* 120: 205-216.

Tye, Michael (1997). "The Problem of Simple Minds: Is There Anything It's Like to Be a Honeybee?" *Philosophical Studies* 88(3): 289-317

Chapter 2

Baars, Bernard (1988). *A Cognitive Theory of Consciousness*. New York: Cambridge University Press.

Baars, Bernard (1997). *In the Theater of Consciousness: The Workspace of the Mind*. Oxford: Oxford University Press.

Baars, Bernard (1998). "Metaphors of Consciousness and Attention in the Brain." *Trends in Neuroscience* 21: 58-62.

Baars, Bernard (2003). "The Global Brainweb: An Update on Global Workspace Theory." Guest Editorial, *Science and Consciousness Review*.

Block, Ned (1995). "On a Confusion about a Function of Consciousness." *Behavioral and Brain Sciences* 18: 227-287.

Brandon, Robert (1997). *Concepts and Methods in Evolutionary Biology*. Cambridge: Cambridge University Press.

Brentano, Franz (1874). *Psychology from an Empirical Standpoint*. London: Routledge and Kegan Paul.

Damasio, Antonio (1989). "Time-locked Multiregional Retroactivation: a Systems-Level Proposal for the Neural Substrates of Recall and Recognition." *Cognition* 33: 25-62.

Dehaene, Stanislas and Naccache, Lionel (2001). "Towards a Cognitive Neuroscience of Consciousness: Basic Evidence and a Workspace Framework." *Cognition* 79: 1-37.

Dennett, Daniel (1991). *Consciousness Explained*. Boston: Little, Brown and Company.

Dretske, Fred (1997). *Naturalizing The Mind*. Cambridge: MIT Press.

- Edelman, Gerald (1989). *Neural Darwinism*. New York: Basic Books.
- Edelman, Gerald. (2003). "Naturalizing Consciousness: A Theoretical Framework." *Proceedings of the National Academy of Sciences* 100(9): 5520-5524.
- Flynn, William (1962). "Visual Hallucinations in Sensory Deprivation." *Psychiatric Quarterly* 36(1): 55-65.
- Gould, Stephen Jay and Lewontin, Richard (1979). "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." *Proceedings of the Royal Society of London* 205: 581-598.
- Grantham, Todd and Nichols, Shaun (2000). "Adaptive Complexity and Phenomenal Consciousness." *Philosophy of Science* 67, 648-670.
- John, Erwin Roy (1976). "A Model of Consciousness." In Schwartz, Gary and Shapiro, David (eds.), *Consciousness and Self-Regulation*. New York: Plenum Press.
- John, Erwin Roy (2001). "A Field Theory of Consciousness." *Consciousness and Cognition* 10(2): 184-213.
- Johnston, William and Dark, Veronica (1986). "Selective Attention." *Annual Review of Psychology* 37: 43-75.
- Kanwisher, Nancy (2001). "Neural Events and Perceptual Awareness." *Cognition* 79: 89-113.
- Kihlstrom, John (1987). "The Cognitive Unconscious." *Science* 237(18): 1445-1452.
- Langer, Ellen and Imber, Lois (1979). "When Practice Makes Imperfect: Debilitating Effects of Overlearning." *Journal of Personality and Social Psychology*, 37(11): 2014-2024.
- Morsella, Ezequiel (2005). "The Function of Phenomenal States: Supramodular Interaction Theory." *Psychological Review* 112: 1000-1021.
- Murphy, Sheila and Zajonc, R. B. (1993). "Affect, Cognition and Awareness: Affective Priming with Optimal and Suboptimal Stimulus Exposures." *Journal of Personality and Social Psychology* 64(5): 723-739.
- Robinson, Richard (2009). "Exploring the 'Global Workspace' of Consciousness." *PLoS Biology* 7 (3): e1000066.
- Rockwell, Teed (1997). "Global Workspace or Pandemonium?" *Journal of Consciousness Studies* 4(4): 334-337.

- Rozin, Paul (1976). "The Evolution of Intelligence and Access to the Cognitive Unconscious." In Sprague, James and Epstein, Alan (eds.), *Progress in Psychobiology and Physiological Psychology*. New York: Academic Press.
- Spelke, Elizabeth (2003). "What Makes Us Smart? Core Knowledge and Natural Language." In Gentner, Dedre and Goldin-Meadow, Susan. *Language in Mind: Advances in the Study of Language and Thought*. Cambridge: MIT Press.
- Stoerig, Patricia and Cowey, Alan (1997). "Blindsight in Man and Monkey." *Brain* 120(3): 535-559.
- Squire, Larry (1992). "Declarative and Nondeclarative Memory: Multiple Brain Systems Supporting Learning and Memory." *Journal of Cognitive Neuroscience* 4(3), 232-243.
- Tye, Michael (1997). "The Problem of Simple Minds: Is There Anything It Is Like to Be a Honey Bee?" *Philosophical Studies* 88: 289-317.
- Tulving, Endel and Schacter, Daniel (1990). "Priming and Human Memory Systems." *Science* 247(4940): 301-306.
- Wegner, Daniel (1989). *White Bears and Other Unwanted Thoughts: Suppression, Obsession and the Psychology of Mental Control*. New York: Viking Books.
- Wilson, Timothy and Schooler, Jonathan (1991). "Thinking Too Much: Introspection Can Reduce the Quality of Preferences and Decisions." *Journal of Personality and Social Psychology* 60: 181-192.

Chapter 3

- Allen, Colin and Bekoff, Marc (1999). *Species of Mind: The Philosophy and Biology of Cognitive Ethology*. Cambridge: MIT Press.
- Baars, Bernard (2003). "The Fundamental Role of Context: Unconscious Shaping of Conscious Information." In Baars, Bernard; Banks, William; and Newman, James (eds.), *Essential Sources in the Scientific Study of Consciousness*. Cambridge: MIT Press.
- Bechtel, William (2003). "Modules, Brain Parts, and Evolutionary Psychology." In Scher, Steven and Rauscher, Frederick (eds.), *Evolutionary Psychology: Alternative Approaches*. Norwell: Kluwer Academic.
- Clark, Robert, and Squire, Larry (1998). "Classical Conditioning and Brain Systems: The Role of Awareness." *Science* 280 (5360): 77-81.
- Clark, Robert; Manns, Joseph and Squire, Larry (2002). "Classical Conditioning, Awareness,

and Brain Systems.” *Trends in Cognitive Sciences*: 6(12): 524-531.

Cohen, Neal; Poldrack, Russell, and Eichenbaum, Howard (1997). “Memory for Items and Memory for Relations in the Procedural/Declarative Memory Framework.” *Memory*, 5 (1): 131-178.

Fodor, Jerry (1983). *The Modularity of Mind*. Cambridge: MIT Press.

Gallistel, Charles (1993). *The Organization of Learning*. Cambridge: MIT Press.

Griffin, Donald (1991). “Progress Toward a Cognitive Ethology.” In Ristau, Carolyn (ed.), *Cognitive Ethology: The Minds of Other Animals*. Hillsdale: Lawrence Erlbaum.

Griffin, Donald (2001). *Animal Minds*. Chicago: University of Chicago Press.

Johnson, Marcia (1983). “A Multiple-Entry, Modular Memory System.” In Bower, Gordon (ed.), *The Psychology of Learning and Motivation: Advances in Research and Theory* (Vol. 17, pp. 81-123). New York: Academic Press.

Nesse, Randolph and Lloyd, Alan (1992). “The Evolution of Psychodynamic Mechanisms,” in Barkow, Jerome et al. (eds.), *The Adapted Mind*. Oxford: Oxford University Press.

Posner, Michael and Snyder, C.R.R. (1975). “Attention and Cognitive Control.” In Solso, Robert (ed.), *Information Processing and Cognition: The Loyola Symposium*. Hillsdale, NJ: Lawrence Erlbaum Associates Inc.

Roitblat, Herbert and von Fersen, Lorenzo (1992). “Comparative Cognition: Representations and Processes in Learning and Memory.” *Annual Review of Psychology* 43: 671-710.

Schacter, Daniel (1989). “On the Relation Between Memory and Consciousness: Dissociable Interactions and Conscious Experience.” In Roediger, Henry and Craik, Fergus (eds.), *Varieties of Memory and Consciousness: Essays in Honor of Endel Tulving*. Hillsdale, NJ: Erlbaum Associates.

Shettleworth, Sara (1998). *Cognition, Evolution and Behavior*. New York: Oxford University Press.

Shiffrin, Richard and Schneider, Walter. (1977) “Controlled and Automatic Information Processing: II. Perception, Learning, Automatic Attending and a General Theory.” *Psychological Review* 84: 125 190.

Walker, Stephen (1983). *Animal Thought*. London: Routledge and Kegan Paul.

Wynne, Clive (2001). *Animal Cognition: The Mental Lives of Animals*. New York: Palgrave

Press.

Chapter 4

- Allen-Hermanson, Sean (2008). "Insects and the Problem of Simple Minds: Are Bees Natural Zombies?" *Journal of Philosophy* 105(8): 389-415.
- Baars, Barnard (2005). "Subjective Experience is Probably Not Limited to Humans: The Evidence from Neurobiology and Behavior." *Consciousness and Cognition* 14(1): 7-21.
- Bitterman, Jeff (1996). "Comparative Analysis of Learning in Honeybees." *Animal Learning and Behavior* 24(2): 123-141.
- Brown, Culum and Laland, Kevin (2003). "Social Learning in Fishes: A Review." *Fish and Fisheries* 4:280-288.
- Brown, Culum; Laland, Kevin and Krause, Jens (2006). *Fish Cognition and Behavior*. Oxford: Blackwell Publishing, Ltd.
- Bshary, Redouan; Wickler, Wolfgang; and Fricke, Hans (2002). "Fish Cognition: A Primate's Eye View." *Animal Cognition* 5:1-13.
- Bugnyar, Thomas and Heinrich, Bernd (2005). "Ravens, *Corvus corax*, Differentiate Between Knowledgeable and Ignorant Competitors." *Proceedings of the Royal Society* 272(1573): 1641-1646.
- Bullock, Theodore and Horridge, Adrian (1965). *Structure and Function of the Nervous System of Vertebrates*. San Francisco: Freeman Press.
- Burghardt, Gordon (1977). "Learning Processes in Reptiles." In Gans, Carl and Tinkle, Daniel (eds.), *Biology of the Reptilia: Ecology and Behavior*. New York: Academic Press.
- Butler, Ann; Manger, Paul; Lindahl, B.I.B. and Århem, Peter (2005). "Evolution of the Neural Basis of Consciousness: A Bird-Mammal Comparison." *Bioessays*, 27: 923-936.
- Carew, Thomas and Sahley, Carrie (1986). "Invertebrate Learning and Memory: From Behavior to Molecules." *Annual Review of Neuroscience*, 9:435-487.
- Carter, David and Eckerman, Carter (1975). "Symbolic Matching by Pigeons: Rate of Learning Complex Discriminations Predicted from Simple Discriminations." *Science* 187(4117): 662-664.
- Couvillon, Patricia and Bitterman, Jeff (1980). "Some Phenomena of Associative Learning in Honeybees." *Journal of Comparative and Physiological Psychology* 94(5): 878-885.

- Dole, Jim; Rose, Betty; and Tachiki, Ken (1981). "Western Toads (*Bufo boreas*) Learn Odor of Prey Insects." *Herpetologia* 37: 63-67.
- Eccles, John (1992). "Evolution of Consciousness." *Proceedings of the National Academy of Science, USA* 89: 7320-7324.
- Edelman, David; Baars, Bernard; and Seth, Anil (2005). "Identifying Hallmarks of Consciousness in Non-Mammalian Species." *Consciousness and Cognition* 14: 169-187.
- Finn, Julian; Tregenza, Tom; and Norman, Mark (2009). "Defensive Tool Use in a Coconut-Carrying Octopus." *Current Biology* 19(23): R1069-R1070.
- Fiorito, Graziano and Scotto, Pietro (1992). "Observational Learning in *Octopus vulgaris*." *Science* 256(5056): 545-547.
- Funayama, E.Sumie; Couvillon, Patricia and Bitterman, Jeff (1995). "Compound Conditioning in Honeybees: Blocking Tests of the Independence Assumption." *Animal Learning and Behavior*. 23(4): 429-437.
- Giuditta, Antonio; Libonati, Massimo; Packard, Andrew and Prozzo, Niccola (1971). "Nuclear Counts in the Brain Lobes of *Octopus vulgaris* as a Function of Body Size." *Brain Research* 25(1): 55-62.
- Gould, Steven (1996). "Specializations in Honey Bee Learning." In Moss, Cynthia and Shettleworth, Sarah (eds.), *Neuroethological Studies of Cognitive and Perceptual Processes*. Boulder: Westview Press.
- Griffiths, Daniel; Dickinson, Anthony; and Clayton, Nicola (1999). "Episodic Memory: What Can Animals Remember About Their Past?" *Trends in Cognitive Science* 3(2): 74-80.
- Hanlon, Roger, and Messenger, John (2002). *Cephalopod Behavior*. Cambridge: Cambridge University Press.
- Helfman, Gene and Schultz, Eric (1984). "Social Transmission of Behavioral Traditions in a Coral Reef Fish." *Animal Behavior* 32: 379-384.
- Hochner, Binyamin; Shomrat, Tal and Fiorito, Graziano (2006). "The Octopus: A Model for a Comparative Analysis of the Evolution of Learning and Memory Mechanisms." *The Biological Bulletin* 210: 308-317.
- Hodos, William and Campell, Bernard (1966). "Scala Naturae: Why There is no Theory in Comparative Psychology." *Psychological Review* 76: 337-350.

- Hvorecny, Lauren; Grudowski, Jessica; Blakeslee, Carrie; Simmons, Tiffany; Roy, Paula; Brooks, Jennifer; Hanner, Rachel; Beigel, Marie; Karson, Miranda; Nichols, Rachel; Holm, Johanna and Boal, Jean (2007). "Octopuses and Cuttlefishes Can Conditionally Discriminate." *Animal Cognition* 10(4): 449-459.
- Jarvis, Erich et al. (2005). "Avian Brains and a New Understanding of Vertebrate Brain Evolution." *Nature Reviews Neuroscience* 6: 151-159.
- Jerison, Harry and Barlow, Horace (1985). "Animal Intelligence as Encephalization (and Discussion)." *Philosophical Transactions of the Royal Society of London B* 308(1135): 21-35.
- Kardong, Kenneth (1995). *Vertebrates: Comparative Anatomy, Function and Evolution*. Dubuque, Iowa: W.C. Brown.
- Kieffer, James and Colgain, Patrick (2004). "The Role of Learning in Fish Behavior." *Reviews in Fish Biology and Fisheries* 2(2): 125-143.
- Kuba, Michael; Meisel, Daniela; Byrne, Ruth., Griebel, Ulrike and Mather, Jennifer (2003). "Looking at Play in *Octopus vulgaris*." *Berliner Paläontologische Abhandlungen* 3: 163-169.
- Maldonado, Harry (1968). "Effects of Electroconvulsive Shock on Memory in *Octopus vulgaris*." *Zeitschrift für vergleichende Physiologie*. 63: 113-118.
- Maldonado, Harry (1969). "Further Investigations on the Effect of Electroconvulsive Shock on Memory in *Octopus vulgaris*." *Zeitschrift für vergleichende Physiologie* 68: 60-71.
- Mather, Jennifer and Anderson, Richard (1999). "Exploration, Play, and Habituation in Octopuses." *Journal of Comparative Psychology*, 113: 333-338.
- Mather, Jennifer (2008). "To Boldly Go Where No Mollusc Has Gone Before: Personality, Play, Thinking and Consciousness in Cephalopods." *American Malacological Bulletin* 24: 51-58.
- Mather, Jennifer (2009). "Home Choice and Modification by Juvenile *Octopus vulgaris*: Specialized Intelligence and Tool Use?" *Journal of Zoology* 233(3): 359-368.
- Menzel, Randolph and Erber, Joachim (1978) "Learning and Memory in Bees." *Scientific American*, 239(1): 102-110.
- Messenger, John (1977). "Prey-capture and Learning in the Cuttlefish, *Sepia*." *Symposia of the Zoological Society of London* 38: 347-376.

- Nelson, Thomas (1996). "Consciousness and Metacognition." *American Psychologist* 51: 102-116.
- Nelson, Thomas and Narens, Louis (1996). "Why Investigate Metacognition?" In Metcalfe, Janet and Shimamura, Arthur (eds), *Metacognition*. Cambridge: MIT Press.
- Papini, Mauricio and Bitterman, Jeff (1991). "Appetitive Conditioning in *Octopus cyanea*." *Journal of Comparative Psychology* 105(2): 107-114.
- Paradis, Sébastien and Cabanac, Michel (2004). "Flavor Aversion Learning Induced by Lithium Chloride in Reptiles but not in Amphibians." *Behavioral Processes* 67(1): 11-18.
- Pepperberg, Irene (2006). "Cognitive and Communicative Abilities of Grey Parrots (*Psittacus erithacus*)." In Leuschner, Andrew (ed.), *Parrot Behavior*. Cambridge: MIT Press.
- Powell, Donald and Churchwell, Donald (2002). "Mediodorsal Thalamic Lesions Impair Trace Eyeblink Conditioning in the Rabbit." *Learning and Memory* 9: 10-17.
- Powers, Irene (1990). "Brain Mechanisms of Learning in Reptiles." In Kesner, Raymond and Olton, David (eds.) *The Neurobiology of Comparative Cognition*. Hillsdale: Lawrence Erlbaum.
- Proust, Joëlle (2003) "Does Metacognition Necessarily Involve Metarepresentation?" *Behavioral and Brain Sciences* 26: 352.
- Ristau, Carolyn (1991). "Aspects of the Cognitive Ethology of an Injury-Feigning Bird, the Piping Plovers." In Ristau, Carolyn (ed.), *Cognitive Ethology: The Minds of Other Animals. Essays in Honor of Donald R. Griffin*. Hillsdale, NJ: Lawrence Erlbaum.
- Roitblat, Herbert and von Fersen, Lorenzo (1992). "Comparative Cognition: Representations and Processes in Learning and Memory." *Annual Review of Psychology* 43: 671-710.
- Rogers, Lesley and Kaplan, Gisela (2004). *Comparative Vertebrate Cognition: Are Primates Superior to Non-Primates?* New York: Kluwer Academic.
- Reilly, Steve and Good, Mark (1989). "Hippocampal Lesions and Associated Learning in the Pigeon." *Behavioral Neuroscience* 103(4): 731-742.
- Smith, J. David; Shields, Wendy and Washburn, David (2003). "The Comparative Psychology of Uncertainty Monitoring and Metacognition." *Behavioral and Brain Sciences* 26: 317-373.
- Smith, J. David; Shields, Wendy and Washburn, David (2008). "The Comparative Study of Metacognition: Sharper Paradigms, Safer Inferences." *Psychonomic Bulletin and Review* 15: 679-691.

- Suboski, Milton (1992). "Releaser-Induced Recognition Learning by Amphibians and Reptiles." *Animal Learning and Behavior* 20(1): 63-82.
- Sutherland, N.S. (1960). "Theories of Shape Discrimination in Octopus." *Nature*. 186: 840-844.
- Takehara, Kaori; Kawahara, Shinegori; Takatsuki, Kanako; and Kirino, Yuraka (2002). "Time-limited Role of the Hippocampus in the Memory for Trace Eyeblink Conditioning in Mice." *Brain Research* 951(2): 183-190.
- Thomson, P.A. And Boice, R. (1975). "Attempts to Train Frogs: Review and Experiments." *Journal of Biological Psychology* 17: 3-13.
- Watve, Milind; Thakar, Juilee; Kale, Abhijit; Puntambekar, Shweta; Shaikh, Imran; Vaze, Kaustubh; Jog, Maithili and Paranjape, Sharayu (2002). "Bee-eaters (*Merops orientalis*) Respond to What a Predator Can See." *Animal Cognition* 5(4): 253-259.
- Weiss, Craig; Bouwmeester, Hans; Power, John; and Disterhoft, John (1999). "Hippocampal Lesions Prevent Trace Eyeblink Conditioning in the Freely Moving Rat." *Behavioral Brain Research* 99: 123-132.
- Woody, David and Mathis, Alicia (1998). "Acquired Recognition of Chemical Stimuli from an Unfamiliar Predator: Associative Learning by Adult Newts, *Notophthalmus viridescens*." *Copeia* 4: 1027-1031.
- Wynne, Clive (2001). *Animal Cognition*. New York: Palgrave.
- Wynne, Clive and McLean, Ian (1999). "The Comparative Psychology of Marsupials." *Australian Journal of Psychology* 51(2): 111-116.
- Zentall, Thomas; Clement, Tricia; Bhatt, Ramesh and Allen, Jessica (2001). "Episodic-Like Memory in Pigeons." *Psychonomic Bulletin and Review* 8: 685-690.

Chapter 5

- Barr, Stuard; Laming, Peter; Dick, Jaimie, and Elwood, Robert (2007). "Nociception or Pain in a Decapod Crustacean?" *Animal Behavior* 75(3): 745-751.
- Bateson, Patrick (1991). "Assessment of Pain in Animals." *Animal Behavior* 42(5): 827-839.
- Bekoff, Alan (2003). "Considering Animals – Not 'Higher' Primates." *Zygon* 38(2): 229-245.
- Bentham, Jeremy (1823). *Introduction to the Principles of Morals and Legislation*, second edition.

- Bennett, R. Avery (1991). "A Review of Anesthesia and Chemical Restraint in Reptiles." *Journal of Zoo and Wildlife Medicine* 22(3): 282-303.
- Blanke, Olaf and Metzinger, Thomas (2008). "Full-Body Illusions and Minimal Phenomenal Selfhood." *Trends in Cognitive Science* 13(1): 7-13.
- Carruthers, Peter (2000). *Phenomenal Consciousness*. Cambridge: Cambridge University Press.
- DeGrazia, David (1996). *Taking Animals Seriously: Mental Life and Moral Status*. Cambridge: Cambridge Press.
- Korsgaard, Christine (forthcoming). "Facing the Animal You See in the Mirror." *Harvard Review of Philosophy* 16: 2-7.
- Machin, Karen (1999). "Amphibian Pain and Analgesia." *Journal of Zoo and Wildlife Medicine* 30(1): 2-10.
- Pepperberg, Irene; Garcia, Sean; Jackson, Eric and Marconi, Sharon (1995). "Mirror Use in African Grey Parrots." *Journal of Comparative Psychology* 109(2): 182-195.
- Regan, Tom (1983). *The Case for Animal Rights*. Berkeley: University of California Press.
- Rutherford, Kenneth (2002). "Assessing Pain in Animals." *Animal Welfare* 11(1): 31-53.
- Singer, Peter (1975). *Animal Liberation*. London: Pimlico.
- Sneddon, Lynne (2003). "The Evidence for Pain in Fish: The Use of Morphine as an Analgesic." *Applied Animal Behavior Science* 83(2): 153.
- Verhoog, Henk and Visser, Thijs (1997). "A View of Intrinsic Value Not Based on Animal Consciousness." In Dol, Marcel; Kananmotalib, Soemini; Lijmbach, Susanne; Rivas, Esteban and van den Boos, Ruud (Eds.) *Animal Consciousness and Animal Ethics: Perspectives from the Netherlands*. Assen: Van Gorcum.
- Wise, Steven (2002). *Drawing the Line: Science and the Case for Animal Rights*. Cambridge, MA: Perseus Publishing.