A Framework for Investigating Animal Consciousness

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Abstract An assessment of consciousness in nonverbal animals requires a framework for research that extends testing methods beyond subjective report. This chapter proposes a working definition of consciousness in terms of temporal representation that provides the critical link between internal phenomenology and external behavior and neural structure. Our claim is that consciousness represents the present moment as distinct from the past and the future in order to flexibly respond to stimuli. We discuss behavioral and neural evidence that indicates the capacity for both flexible response and temporal representation, and we illustrate these capacities in fish, a taxonomic group that challenges human intuitions about consciousness.

Keywords Animals · Behavior · Consciousness · Fish · Flexibility · Goal-directed · Pain · Temporal representation · Telencephalon · Tool use

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Highlights

- consciousness defined in terms of teleosemantic theory of temporal representation,
- temporal representation links phenomenology, behavior, and neural structure,
- four forms of evidence indicate temporal representation and flexible response,
- three neural structures essential,
- capacities of fish considered as test of framework.

The question is not, Can they reason, nor Can they talk, but Can they suffer? Bentham (1789).

This oft-quoted statement succinctly captures the central insight of utilitarian ethics: the capacity to feel pain ought to be the primary marker of moral concern rather than the capacity for abstract reasoning.[1] Rationality may be necessary to be a moral *agent,* but it is not required to be a moral *subject*. The force of this insight goes well beyond utilitarianism and strikes at the heart of an ethical relationship to the world. A crying infant compels care, an injured pet elicits sympathy. In humans, the evolutionarily adaptive capacity for empathy is so well developed that viewers of animated geometric figures will interpret them as agents feeling fear, love, and anger (Heider and Simmel 1944). Of course, animated circles do not suffer, which raises the problem of gauging appropriate ethical response. On one hand, concern for suffering requires that we minimize pain in all cases, but on the other hand, the tendency to overextend this empathetic concern means we need some measures other than our own moral feelings to determine which animals do in fact suffer.

To begin with, we can distinguish three elements in human suffering: sensory responsiveness to noxious stimuli, conscious hurtfulness, and self-conscious understanding of the pain's significance.[2] While each of these elements raises difficult research issues, this chapter will focus on conscious hurtfulness as the *sin qua non* of suffering. Conscious pain is the element in human suffering that we attribute to infants and pets and circles; it is the element that calls for an ethical response.

To determine which animals suffer, then, we need to determine which animals are conscious. In the following, we propose a working definition of consciousness in terms of temporal representation that links internal phenomenology with behavioral function and neural structure. It is worth emphasizing that the proposal offers a *working* definition of consciousness. Temporal representation is a necessary feature of consciousness, we claim, and is sufficient to distinguish conscious

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[1] This is not to say that the capacity to feel pain is the only marker for moral concern. Suffering is one very important marker but should figure within a broader ethical theory.

[2] A fourth element could, and perhaps should, be added: the emotional response. The conscious feeling of dislike rivals conscious hurtfulness as the most important feature of suffering. As with pain, conscious rather than unconscious emotions are associated with suffering, so the investigation of consciousness is appropriate in both cases.

from unconscious representations. For a complete account, more must be said about what conditions are necessary for something to be a "representation," among other things.[3] As a working definition, the test of its value is its usefulness in providing an explanation that accounts for the available data. Phenomenological experience forms the foundational data; it is the data that characterizes consciousness from the subjective perspective. Comparative behavioral and neuropsychological evidence characterize consciousness from the objective perspective. A working definition of consciousness is useful to the extent that it brings these two perspectives into alignment and offers testable hypotheses for the future research. We are particularly interested in the research potential of the present proposal and hope the debate about animal consciousness sparks refinement of the theory as well as methodological recommendations for effective tests. If we have more effective means of knowing when animals are suffering, we can more effectively decide what moral response is appropriate. Ideally, the science of consciousness can provide a useful guide for our moral intuitions.

1 Defining Consciousness

The first, and probably most difficult task in this project is to set out a workable operational definition of consciousness. The point here is not to set out necessary and sufficient conditions of the sort proposed in conceptual analysis. Our goal is to identify a tractable target for scientific research, to map *the way a creature experiences the world* to *the world it is experiencing*. For as many years as philosophers have been writing about this topic, the best description of the way a creature experiences the environment around it has been the unhelpful locution "what it's like" to sense red or feel pain (Nagel 1974; Block 1995; Chalmers 1997; Lycan 1996). Though vague, the phrase resonates because it points to the elusive quality that distinguishes an awake state that is responsive to sensory stimuli from fully unconscious states such as dreamless sleep. When unconscious, there is clearly nothing it is like to sense red or feel pain. Similarly, there is nothing it is like to be an object incapable of consciousness, like a table or a laptop computer. For us, by contrast, waking life is full of sights and sounds and tastes and smells which combine and shift to form a vibrant, changing world, and there is something it is like to experience that world. Later we will say more to refine this rough contrast into a sufficient working definition. Even in us, awake responses to stimuli are often unconscious. Consider, for example, your current body position. To maintain balance and prevent injury, you need to shift position periodically in response to proprioceptive signals. Until your attention was drawn to your body,

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[3] Though the account is compatible with various theories of representation, we favor a teleofunctional view. For more, see footnote 6.

chances are that these shifts in position were accomplished unconsciously. There was “nothing it was like” for you to shift your body position.

But “what it’s like” merely points at the target phenomenon without adequately identifying it. One tempting refinement of “what it’s like” would be to assume it is a case of self-consciousness. Of course, the instant we begin to think about the nature of consciousness, we become self-conscious by means of introspection. Consciousness cannot be caught unawares, as it were, and this fact raises several methodological difficulties in designing experiments to test human consciousness. Whenever a researcher asks a subject to report on her conscious experience, she must introspect in order to do so. Consequently the capacity for self-consciousness and consciousness appear inseparable. In the investigation of non-human animal consciousness, however, the separability of consciousness and self-consciousness is more clearly apparent. To be conscious of one’s self requires an ability to distinguish one’s self from other selves.[4] More than the simple recognition that one’s body is unique with regard to sensation and action, self-consciousness involves the recognition that one has a unique *mind*. The representation of a unique mind involves, at minimum, a theory of mind, including an understanding of deception, perceptual processes, and empathetic imagination (Perner 1991; Gopnik 1993; Tomasello 1999; Goldman 2006). Given the sophisticated representational abilities required for self-consciousness, it seems likely that consciousness evolved prior to self-consciousness, and so we should expect there to be creatures capable of consciousness that are not capable of self-consciousness. There may be reasons to claim that consciousness entails self-consciousness, but this necessary link must be argued and not assumed.

So far then, we can say that we are looking for a phenomenon that occurs during awake states that are responsive to sensory stimuli, and there is something it is like to be in those states. This definition is insufficient for a science of consciousness. The problem is that it is unclear how to supplement it without begging the question about the nature of consciousness. If we propose that consciousness is a global workspace (Baars 1988, 1997; Baars and Newnan 1994; Dehaene and Naccache 2001; Dehaene and Changeux 2011), this assumes a particular integration function is constitutive of consciousness. If we suggest that consciousness involves being conscious of our mental states, the assumption is that some form of higher-order state is necessary for consciousness.[5] Nonetheless, some starting

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[4] At least, this is what we mean by ‘self-consciousness’ here: conscious states about one’s own mental states. Conscious bodily states form a ‘minimal phenomenal self’ (Metzinger 2009) or a core self (Damasio 1999) but they are not self-conscious on our use of the term.

[5] According to higher-order theories of consciousness, a mental state is conscious when there is another mental state that is conscious of it. The appropriate higher-order state might be a thought or a sensation, it might be extrinsic or intrinsic to the lower-order state, and it might be occurrent or dispositional. The theory is higher-order because the relation is a consciousness of consciousness; two levels of consciousness are required (Lycan 1996, 2004; Carruthers 2000, 2004; Rosenthal 2005; Kriegel 2006, 2009; Gennaro 2006, 2012). Theories that involve cognitively higher-order capacities such as conceptual or inferential abilities are not higher-order theories in the sense invoked by higher-order theories of consciousness.

assumption about the nature of consciousness is necessary to articulate a clear target for scientific explanation.

We believe that the phenomenologist Husserl (1905) offered a useful suggestion when he noted the essential role of time in the structure of consciousness. According to Husserl, consciousness represents the world from the perspective of a now-point. We take the items presented to us by consciousness as before us now. Yet this moment is not instantaneous, it includes a brief span of time from just past (retention) to just ahead (protention). A span is necessary to account for the experience of duration, such as the hum of cicadas or the waving of leaves in the breeze. In other words, an essential aspect of what it is like to sense the world is to sense it as now enduring (Droege 2003, 2009).

The representation of time in consciousness differs crucially from the way representations may vary in relation to time. A creature that can vary its action in accord with the seasons or other natural temporal patterns does not need to represent time, it simply needs to respond to the appropriate temporal cues. Even a perception–action sequence that includes a temporal element utilizes time without representing it. The marine Palolo worm *Eunice viridis,* for example, times its reproductive cycle to a 2-h period in late fall. The precise synchronization of thousands of these organisms is attributable to a combination of biologically based oscillations (daily, annually, lunar, and tidal).[6] As long as action is strictly coded to some sort of fixed cycle, no representation *of* time is required. Only when a creature might decide between actions must it be able to assess the environment *as it is now* in order to determine how to proceed in the light of its goals. As we will argue, the evolutionary development of flexible behavior demands the ability to represent time. This psychological connection between flexibility and temporal representation along with the proposed definitional connection between temporal representation and consciousness form the links between private experience and public action necessary for assessing the capacity for consciousness in non-human animals.

This claim is controversial, and thus forms a substantive commitment about the nature of consciousness, just as the claim that consciousness is a global workspace or a higher-order state (Baars 1997, 2003; Rosenthal 2005; Dehaene and Changeux 2011). Nonetheless, this description of consciousness has several advantages over other proposed claims. First, unlike the global workspace, our sense of presence is phenomenologically apparent. The world appears before us as *right here, right*

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[6] Gallistel (1990, p. 236). Later Gallistel notes that "the ability to detect and make behavioral use of temporal intervals of arbitrary duration is distinct from the ability to record the time at which something happens" (240). Early on in the book, he also offers a useful definition of 'representation' as "a functioning isomorphism between an aspect of the environment and a brain process that adapts an animal's behavior to it" (3). For a fully developed theory of the biological functional value of representation, see Millikan (1984, 1993, 1998, 2004). Because biological function is necessary to representation on the view we are proposing, a time code cannot simply be added to a computer to make it conscious. A prior question must be answered: whether and how a computer or robot might be capable of genuine representation rather than derived representation (Searle 1980).

now. What it is like to be conscious includes the temporal immediacy of experience. Note that the coordination of sensations and thoughts into a representation of presence is consistent with the integration function proposed by global workspace theorists and other neuroscientific theories of consciousness (Edelman and Tononi 2000; Gulick 2004; Tononi 2004, 2008; Tononi and Koch 2008; Dehaene and Changeux 2011). The present proposal puts the integration function into an evolutionary and developmental context to explain why creatures come to integrate information in the particular form that is conscious representation. A second, related advantage is that the identification in nonhuman animals of the ability to represent the present moment offers an intermediate evolutionary step between simple sensory response and more sophisticated higher-order representation. As noted above, self-consciousness requires additional evolutionary pressure to develop beyond the capacity for consciousness.

In the remainder of this chapter, we will consider the behavioral and physical evidence for temporal representation, and we have chosen to focus on fish as a particularly hard case for demonstrating consciousness (Braithwaite 2010). Fundamental differences between fish and humans stretch the argument from analogy to its breaking point, and this relative weakness places more weight on functional and theoretical argument. If we can make a convincing case that fish are conscious, despite our lack of intuitions about what it might be like to be them, then we can be sure that the framework of explanation is supporting the theory rather than mere anthropocentric inference.

In sum, conscious states are those it is like something to have. When we are awake and responsive to sensory stimuli, there is something it is like to experience (some of) those sensations. Furthermore, our conscious sensory experience presents the world as appearing before us *now*, which includes a brief temporal span of events indicating an enduring environment. While temporal representation is not (yet) universally accepted as a criterion for consciousness, we aim to show that it forms a vital part of a research program to establish a framework for consciousness in non-human animals.

2 Behavioral Function

Behavior is certainly the primary and most potent indicator of mental activity, even if it cannot provide a complete explanation of the mind and its capacities. Dogs, cats, horses, and rabbits behave in ways similar to the ways we behave when excited, fearful, happy, or in pain (Fraser 2009). As a result, it is fairly easy to believe that these creatures have similar mental states. When they are awake and responsive to sensory stimuli, it seems reasonable to assume there is something it is like for them to experience their sensations, i.e., they have conscious states.

To reinforce the earlier claim that consciousness and self-consciousness are separate capacities, note that there is no compelling reason to attribute self-consciousness to these creatures. When the squirrels look to be enjoying their game of chase in the tree, it is difficult to imagine that there is nothing it is like for them to *consciously feel* the joy of their game. However, it is not at all difficult to imagine that they lack the reflective ability to think of themselves *as* squirrels or *as* joyful. They may very well be joyful without reflecting self-consciously on their joy. Our ability to imagine that a creature is conscious without being self-conscious does not prove these capacities are separable, but it does show that the claim of necessary connection must be argued.

The limits of this strategy of imagining what it is like to be a creature become apparent in the borderline cases. Fish exhibit some similar behavior: their avoidance of electric shocks looks like fear, and their brisk interactions with one another looks like playful fun. But is it? How could we be sure these are not simply automated responses to stimuli in the way a thermostat responds to changes in temperature, or the way our knee reflex responds to the tap of a doctor's rubber hammer?

As the question suggests, we need a way to distinguish automated behavior from conscious response. The ability to flexibly adapt to novel environmental conditions is often taken to signal consciousness (Griffin and Speck 2004; Edelman et al. 2005; Seth et al. 2005; Merker 2005, 2007; Edelman and Seth 2009), but the question is, why? Why should consciousness be connected to flexibility, or indeed to any other behavioral or physiological indicator (Dawkins 2006, 2012)? Here is where the definition of consciousness in terms of the representation of presence can help connect behavior to phenomenology. In order to flexibly respond to a stimulus, a creature must be able to represent the present stimulus environment in relation to its goals. The environment appears in a certain way *now*, and this differs in various ways from the desired environment. There is a predator on the horizon, or no food is available, or scratchy bristles are all around. Without an ability to distinguish how things are now from how things might otherwise be, there is no way to consider alternative paths from here to there. An animal might flee or approach as a simple response to a stimulus, but the ability to consider an alternative possibility involves an assessment of the best action in pursuit of a goal, and this more sophisticated alternative depends on a representation of the present moment. In other words, a representation of *now* is essential to flexible behavior as well as being essential to the structure of consciousness from the first-person perspective.[7]

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[7] Body illusions, such as autoscopic hallucinations and out-of-body experiences, confirm the role of first-person experience in conscious experiences. Even in the strange case of heautoscopic hallucinations where a person experiences her own body and an illusory body from the point of view of both bodies *simultaneously*, the experience is nonetheless from the first-person perspective in the weak sense of an egocentric spatial frame of reference. How there could be two simultaneous egocentric frames of reference is puzzling, as if Escher constructed one of his visually impossible drawings inside the mind. The sense that subjects are 'two selves' suggests these hallucinations form of consciousness (Blanke and Metzinger 2009).

The methodological value of flexibility as behavioral evidence for consciousness lies in the many ways to demonstrate it: (1) differential response to the environment, (2) adaptation to novel situations, (3) manipulation of the environment to accomplish goals, and (4) explicit representation of absent objects.[8] We will consider each form of evidence in terms of how it shows both flexibility and temporal representation. Because all of this evidence demonstrates the same basic capacity, several examples could be used to illustrate more than one form.

As noted earlier, fish are a particularly useful group for this sort of investigation, because they are at the edge of human intuitions about consciousness (Allen 2011). If we can get a framework to guide our thinking and research with fish, then we can make a compelling argument about consciousness in other vertebrates as well, and possibly even invertebrates.

Another reason in favor of studying fish is the wide variety of species and the diverse evolutionary pressures on differential species development. Very closely related species exhibit strikingly different capabilities depending on factors such as the complexity of their environment, density of predators, and availability of resources (Braithwaite 2005). This diversity presents the possibility of tracing correlations in neurobiology, behavior, and environment in much richer ways than are possible in the study of mammals (Kotrschal et al. 1998; Gonzalez-Voyer and Kolm 2010).

Differential response calibrated to relevant differences in a situation is the minimum requirement for flexible behavior; all three of the remaining ways to demonstrate flexibility also show the capacity for differential response. While simple single-celled organisms have the basic ability to react to variations in stimuli, flexibility depends on using information learned in the past to select among different possible actions in the present situation.

Dennett (1995, pp. 373–378) provides a helpful schematic of various ways an organism might be designed to respond successfully to its environment, which he calls the *Tower of Generate-and-Test*. At the base of the tower are *Darwinian creatures*. Gene recombination and mutation provides these creatures a selective advantage, leading to the reproduction of the advantageous genetic traits. The level of *Skinnerian creatures* introduces the element of phenotypic plasticity. The behavior of these creatures can be modified by positive and negative reinforcement. This design system works effectively when a specific response is appropriate given a specific stimulus. When a creature develops the capacity to respond in different ways to a set of stimuli, it becomes a *Popperian creature*. At this level,

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[8] In a recent workshop, Investigating Animal Pain and Consciousness, participants debated the appropriate cognitive marker for consciousness. 'Flexibility' may be too vague to adequately characterize the difference between fixed action patterns and more cognitively complex, variable behavior. Other candidates were explicit knowledge, goal-directed behavior, and decision making. This four-pronged strategy for identifying flexibility further specifies the targeted cognitive ability and incorporates the other candidate suggestions. Adaptation to novel situations involves goal-directed decision making. Manipulation of the environment and explicit representation of absent objects involve explicit knowledge.

a creature no longer simply acts based on past associations; it generalizes on past learning conditions to anticipate which current action will best advance its goals. Associative learning remains the foundation for the generalizations made by Popperian creatures. The critical development is that the associations are no longer one-to-one stimulus–response pairings but become a complex weighting of many-to-many relations. Learning, memory, and crucially, integration of information are necessary to differential response. A creature must be able to determine appropriate behavior based on the assessment of a number of variable factors present in the situation (Merker 2007). Popperian creatures behave flexibly, and so on the proposed account they are conscious.

Consider, for example, the complex symbiotic relationship between the cleaner wrasse *Labroides dimidiatus* and the client fish that need parasites removed. Cleaners establish territorial stations where they feed on the parasites of clients, interacting with clients over 2,000 times a day (Bshary and Grutter 2005). While clients with large home ranges have a choice of several cleaners, they tend to return to the same cleaners, as much or more than 100 times a day (Bshary and Würth 2001). It is in the interest of cleaners, therefore, to provide a valuable service, so clients will continue to return to their station. The mutual benefit of this relationship is complicated by the preference of cleaner fish to feed on the mucus of client fish instead of the parasites. This they do by literally biting a chunk out of the client's flesh, an action that causes the client to visibly shudder. When bitten by a cleaner, clients will respond by chasing the cleaner or by leaving the station (Bshary and Grutter 2005). Another complication is that some of the client fish are predators, so they too have interests that both favor and counter cooperation.

The variety of factors in cleaner–client interactions has resulted in surprisingly sophisticated behavior by the cleaner wrasse, and to a certain extent in cleaner gobies that also perform these services (Bshary and Würth 2001; Bshary and Grutter 2005; Danisman et al. 2010). First, clients may punish cleaners by chasing them or leaving the station. This reaction causes cleaners to limit their cheating in order to avoid these penalties (Bshary and Grutter 2005). Second, cleaners offer incentives to clients in the form of tactile stimulation: a cleaner hovers above the client, touching the client's dorsal fin with its pectoral and pelvic fins (Bshary and Würth 2001). Importantly, cleaners offer tactile stimulation in three sorts of situation: (1) in order to induce clients to stop at the station for a cleaning, (2) differentially to predators over non-predator client fish in order to prevent conflict, and (3) after the cleaner has bitten the client, to prevent the client from chasing or leaving.

A second way to demonstrate flexible behavior is the ability to respond to novel situations by inferring future conditions based on information gathered from the past. This description is loaded with mentally sophisticated terms: inference, past/future conditions, information. To warrant attribution of such cognitively rich abilities requires distinguishing them from the simple weighting of past associations. While past associations necessarily figure in the evaluation of a novel situation, the solution must depend on a combination of features never before experienced simultaneously.

According to the temporal representation theory of consciousness, a representation of the present moment allows the creature to assess the current situation in order to determine which action is the best means toward its goals. If a situation is novel, no merely backward-looking algorithm is sufficient to calculate appropriate behavior. Instead the features of the new situation must be combined. In other words, the creature needs a representation of both feature A and feature B as components of the world *now* in order to know that they need to be combined. The result of this combination specifies the best action in that situation.

The ability of the male cichlids to respond appropriately to a novel set of competitors provides just the sort of cognitively rich inference needed to demonstrate flexible response. Because the species is aggressively territorial, it is useful for them to gain as much information about potential opponents as possible. Watching aggressive interactions is one source of information utilized by cichlids to determine which opponents are more threatening. In an experiment by Grosenick et al. (2007), cichlids were allowed to watch neighbor fish fight with one another in order to determine how much information they were able to gather from observation. Subject fish were shown fights in the following order: A beat B, B beat C, C beat D, and D beat E. In the critical trials, observer fish were placed between super-winner A and super-loser E and between marginally stronger B and marginally weaker D to see how the cichlid would react to these novel pairs. In both cases, the observer cichlid moves toward the weaker fish to assert its dominance.

Because the observer fish has never seen A and E or B and D fight one another, the response cannot be simple association based on past experience. Information about relative fighting strength needs to be assessed given the current opponents in order to determine the best action. This result is particularly striking when the fish identifies D as weaker than B. In this case, both B and D have lost one fight and won one fight, so neither is distinguishable simply as “winner” or “loser.” Only by recognizing B as, in some sense, “winner over C” and D as “loser to C” can the observer act effectively. In other words, the observer fish utilizes memory to identify the relative strength of the particular individuals in the specific current situation. Representation of the features in the world *now* is needed to respond appropriately.

A third behavioral indicator of flexibility is the ability to manipulate the environment in pursuit of a goal. Differential response and assessment of novel situations are both reactive forms of behavior, showing a highly adaptive but not necessarily forward-thinking creature. Proactive, problem-solving skills, in contrast, require the ability to represent how a change in the current environment might bring about the desired goal. In other words, a creature must be able to represent the difference between the current situation and the goal situation in order to determine what action would bring about the appropriate change.

The best example of manipulating the environment is tool manufacture. To fashion a tool requires an understanding of how a goal can be achieved by means of unrelated items. By twisting or bending or combining objects, an animal can produce a tool specifically designed for a particular task. This shows an understanding of the relation between the tool and the task *prior* to the execution of the task. Tool manufacture depends on the ability to plan.

Since fish have no limbs and live in a viscous environment with little gravitational force, they are not likely to demonstrate the capacity to manufacture tools. Twisting and bending just are not in their ecological repertoire. Nonetheless, some features of tool use in fish suggest control over the environment rather than simple reactivity. It is important that the object used as a tool is not itself interesting in any way; its value is only in relation to the final objective. To be tool use, this connection between tool and goal must be clearly evident. Moreover, the creature must refrain from acting on the desired object directly in order to make use of the indirect advantage provided by the tool. An animal changes the relations of things in its environment to accomplish its goal, even though the change in itself is not valued.

Recent evidence suggests that water and stones may be used by fish as tools. Archerfish (*Toxotes* sp.) squirt water at insects sitting on surface plants or flying overhead, and can modify the trajectory and quantity of water proportional to the motion and size of the prey (Schuster et al. 2006; Brown 2012). In the most remarkable and controversial display, a six bar wrasse (*Thalassoma hardwicke*) carries a large food pellet about 75 cm in order to smash it against a specially selected rock to break up the pellets into smaller, digestible pieces (Paśko 2010). This last behavior in particular involves several important steps in problem-solving behavior. First, there is a search for a solution to the problem of breaking down large items of food. Next, the potential solution of using a rock as an anvil is tested until the preferred tool is found. Finally, the selected rock is remembered and reused unless another object proves more effective or convenient.

Caution is advisable in assessing this evidence, since reports are anecdotal, and the behavior has not yet been rigorously investigated.[9] If confirmed, the flexibility in tool use is obvious; no routinized associative stimulus–response pattern could account for the use of a tool to accomplish an otherwise unrelated task. Even if an animal hits upon the value of the tool accidentally, it must be able to remember when and how to use the tool as a means toward its goal. Less obvious is the temporal representation necessary to exhibit this behavior. Problem solving requires that time stops, in a sense. Goal-directed action must cease in order to determine the route forward.[10] Attention to the collection of items in the current environment is geared toward identifying the object or relation of objects needed to achieve the desired end. A creature incapable of stopping time in this way would not be able to solve a problem through the kind of trial and error process exhibited by tool use. Instead, the goal would simply be abandoned and a search for more tractable goal undertaken.

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[9] The definition of "tool use" is also a question. As Brown (2012) points out, most definitions of tool use rule out the use of the substrate as a tool. It seems arbitrary to say that smashing an oyster with a rock is tool use, yet smashing a rock with the oyster is not. The relevant question is whether the action demonstrates controlled manipulation of the environment toward a goal. The way the tool is used indirectly as a means toward the goal is another feature that indicates cognitive flexibility rather than simple conditioned response, whether or not we call it "tool use."

[10] This does not mean that the creature literally freezes in its tracks. The point is that its general, exploratory behavior is not a direct means to its goal. It is a way of determining a means to its goal.

The fourth and last indicator of flexibility is the ability to represent both present features of the situation and features that are absent in the immediate stimulus environment. Any representation of what is present entails the corollary representation of absence. This may seem counterintuitive or even fallacious. There is no reason to assume that my representation of an apple as present before me entails the representation of something else, say a pear, as absent. The point is not that every representation of presence entails the representation of something *in particular* as absent. Rather, the possible contrast case of absence is necessary to make presence meaningful. If I am not capable of representing this apple as *either* present *or* absent, the content "present" adds nothing to the content "apple." In other words, a creature without the capacity for temporal representation of presence *and* absence could represent an apple or a pear or whatever else might be in its environment, but it could not represent the apple *as present*, or *as absent* in the form of a desired but not yet actual goal.

Though this way of putting things may sound too theoretical to be naturalistically viable, the ability to represent goals requires the representation of states of affairs that are not yet the case. Use of spatial memory demonstrates the way successful action often depends on a representation of absent features. Goldfish (*Carassius auratus*) can use landmarks to locate food rewards, even when they approach the landmark from a novel direction (Ingle and Sahagian 1973; Warburton 1990; Rodríguez et al. 1994; Salas et al. 1996). Siamese fighting fish (*Betta splendens*) remember the locations in an eight-arm radial maze that are depleted of food (Roitblat et al. 1982). At high tide gobiid fish (*Bathygobius soporator*) learn the topography of regions surrounding their home pool so that they can jump to an adjacent pool when threatened by a predator during low tide (Aronson 1951, 1971). In all of these cases, appropriate goal-directed behavior indicates that the location of the goal is represented despite its absence from the immediate sensory environment of the fish. Landmarks indicate the absent reward to the goldfish; maze position indicates the presence (and absence) of food to the fighting fish; and the goby springs to safety with no indicators at all save its memory of the position of pools nearby. In each of these cases, the fish discriminates what is now present—the landmark, the maze position, the predator—from what is absent in order to act appropriately to achieve its goals.

These myriad forms of evidence indicate considerable flexibility in fish behavior. A cleaner wrasse will differentially serve or cheat its clients depending on the prospects for reward and punishment. Cichlids react to a novel pair of opponents by inferring their relative fighting strength based on past observations. The six bar wrasse scouts for an ideal rock to break up its food. A goby maps its environment to prepare for an urgent escape. Flexibility depends on an evaluation of the environment as it is now in order to create the environment as it is desired to be. These fish are not simply responding to whatever stimulation appears, they are comparing information about the present situation with information about the past and future in order to respond effectively to the unique demands and prospects of the world as it is now.

3 Neural Structure

To supplement the behavioral evidence for fish consciousness, an examination of neural evidence is the natural next step. But identification of the necessary physical structures for consciousness is tricky. Even in humans, progress on neural correlates of consciousness has been slow and difficult (Metzinger 2000). Reliance on research with mammals assumes that creatures with similar brain structures and functions have similar forms of consciousness. Probably so, but why assume this, and which structures and functions are necessary and sufficient for consciousness? Little theoretical work has been done to justify assumptions that studies on human consciousness apply to nonhuman animals or vice versa. One of the goals of the proposed framework is to help answer these questions.

If the function of consciousness is to represent what is present in order to assess progress toward its goals, a conscious creature's nervous system must do three things. One, it must be capable of acquiring and responding to information about its environment; it must have a sensorimotor system. Two, it must be able to modulate the information it acquires so as to emphasize the goal-related bits and de-emphasize the irrelevant bits; it must have an attentional system. Three, it must be able to selectively act on sensory information; it must have an executive system.

First, a sensorimotor system is the entry-level requirement for mentality of any kind, and certainly for consciousness. The ability to sense and respond appropriately to environmental conditions depends on a representational system that can track beneficial and harmful elements as well as effective and ineffective reactions to them. Recent research has now identified several structures integral to processing pain perception in fish.[11] The same types of nociceptors and specialized fibers that convey information about tissue damage in humans and other mammals have also been described in teleost fish: (1) A-delta fibers are myelinated fibers that are associated with immediate pain; (2) C-fibers are unmyelinated and associated with the longer-lasting form of pain resulting from damage (Sneddon 2002; Sneddon et al. 2003a). The application of noxious stimuli to rainbow trout resulted in diminished appetite, increased evidence of stress (opercula beat rate), and apparent attempts at pain relief by rubbing their snouts on the walls and floor of the tank. Administration of an analgesic has been shown to decrease the negative effect of the noxious stimulus (Sneddon et al. 2003b).

There is also evidence that fish possess the neural structures necessary for rudimentary emotional processes (Braithwaite et al. 2013). Dopaminergic systems essential to reward conditioning, both positively and negatively, have been identified in the fish forebrain (Panula et al. 2010). A section in the fish telencephalon appears to serve the same functional role as the amygdala does in mammals

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[11] 'Pain' here refers to the sensory system that registers physical damage and does not imply consciousness. As noted above, at least two other physiological structures are required for conscious pain in addition to pain sensations. For further discussion of animal pain, see Allen 2004; Allen et al. 2005.

(Rodríguez et al. 2005). When this area is lesioned, for example, fish have difficulty learning to avoid a negative, electric shock (Portavella et al. 2002).

Sensory responsiveness is such an important part of life and mind that it is tempting to think that sensation alone is sufficient for consciousness. The worm wriggles across the hot pavement, and we imagine it feels desperation; the bee sucks on the flower, and we can think of it as happy. Watching environmentally effective and often quite complicated behavior generates in human observers an irresistible empathic identification. We put ourselves in the position of the creature and find it difficult to imagine how such behavior could be produced without consciousness.

This anthropomorphic impulse can be reduced somewhat by reflecting on the complex behaviors we humans do unconsciously. The basic processes supporting any habitual activity—walking, driving, speaking—all occur without conscious direction. We are conscious while exercising these habits but not conscious of the body movements, sensorimotor adjustments, or even the word selection and arrangement necessary to execute everyday skills. Given that quite intricate behavior is often unconscious, what accounts for the difference when sensorimotor activity is conscious?

Here again the definition of consciousness in terms of a representation of presence shows the way forward. Sensorimotor activity is conscious when a creature needs to attend to how its actions in the world as it is *now* will best meet its goals. This means there must be a way to select the important information from all the available ongoing sensations and actions in order to make just that information conscious. So the second physical structure necessary for consciousness is some form of attentional system to relay and modulate sensory input. To serve the modulatory function, ramping up relevant stimuli and dampening irrelevant stimuli, some form of feedback loop or recurrent process is needed. In humans and other primates, a thalamocortical circuit figures in most accounts of the neural correlate of consciousness precisely because it is so effectively modulates neural activity across the entire cortex. Developmental studies of the brain of bony fish (teleosts) suggests that fish have preglomerular-pallial pathways that correspond to areas of the thalamocortical system of mammals, however the function of such areas within the fish brain has yet to be determined. Similarly, the insula-anterior cingulated axis has been considered to play a role in modulating consciousness, but as of yet, it is unclear whether a similar structure is found within the fish brain.

The third necessary function that must be performed by the nervous system of a conscious creature is planning and decision making. As argued in Sect. 3, behavioral flexibility indicates consciousness, and where there is flexibility, there is decision making. Fish have no neocortex, which is the brain structure in mammals that subserves executive functions like planning and decision making. This difference has led some to argue that consciousness in fish is impossible, since a brain area essential to mammalian consciousness does not exist in fish (Rose 2002, 2007). More recent evidence suggests that rather than having a layered neocortical structure, fish have more clustered nuclear regions within the telencephalon that have the capacity for some of the functions seen in the mammalian cortex. Indeed, the telencephalon, or forebrain, of fish is seen as a center where information is integrated (Rodríguez et al. 2005). Despite the presence of structures with some similarity in function to those found in mammals, a simple identification of consciousness with a particular physical substrate implausibly limits the possibility of alternative realizations. On our proposed temporal representation account, any physical structure that instantiates the appropriate sort of representations is thereby conscious. Consequently, the question is not whether fish have a neocortex, the question is whether fish have a structure that is capable of the decision making necessary to differential response to novel situations, manipulation of the environment, and representation of absence.[12] We know from other comparative studies between mammals and birds, these two groups of animals process visual information in very different ways, yet we do not deny either group the capacity to visualize the world around them (Braithwaite and Huntingford 2004).

In fish, the telencephalon is the best candidate to fill the role of the executive system, although evidence is still inconclusive. It has been clearly demonstrated that distinct areas in the fish forebrain are responsible for distinct cognitive capacities such as spatial memory and emotional processing (Portavella et al. 2002; Broglio et al. 2003; Broglio 2005; Dúran et al. 2010; Ebbesson and Braithwaite 2012). Also, the relative size of the telencephalon may indicate greater cognitive capacity in the same way it does in mammals and birds. At least in the case of some fish, a relatively large telencephalon, or forebrain, positively correlates with a complex environment (Kotrschal et al. 1998; Gonzalez-Voyer and Kolm 2010). More research is needed to make a convincing case that telencephalon size, or size of certain nuclei within the telencephalon is a decisive indicator of cognitive capacity. There is some evidence that fish living in structurally more complex environments or ranging over a wider territorial area have relatively larger forebrains (Marchetti and Nevitt 2003; Shumway 2010; Costa et al. 2011). In any case, there must be some structure that supports the sophisticated forms of behavior described in Sect. 2. At this point, the telencephalon is the most likely anatomical substrate of these abilities.

4 Conclusion

The foregoing evidence for flexibility in fish and a physical structure to support it is not meant to be the final word on the question of whether and how fish might be conscious, much less on what the ethical consequences of fish consciousness might

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[12] Cabanac et al. (2009) have offered a similar account utilizing different criteria. They argue that consciousness depends on the ability to assess pleasure and displeasure. While their comparative and evolutionary account is amenable to the approach we advocate, “pleasure” is too broad a term to effectively isolate all and only conscious states. Pleasurable things may motivate me unconsciously, as when I find myself at the ice cream store again. Neutral things may be consciously represented as well, if there is nothing more interesting going on *now*.

be. It is meant to be the beginning of a cross-disciplinary debate about the sort of framework that will best organize the growing body of data on behavior, development, and anatomy of fish and other nonhuman animals in order to assess the capacity for consciousness. Once we have a means of determining what sorts of animals feel conscious pain, we can more effectively think about ways to minimize or eliminate their suffering.

What we offer here is an operational definition of consciousness in terms of temporal representation, in particular in terms of the phenomenological experience of the world *as present*. Our suggestion is that the representation of presence explains why behavioral flexibility is good evidence for consciousness. In order to respond differentially to the present situation, a creature must be able to identify the salient features of the world *now* as distinct from the way things have been or are desired to be. This critical link between how the world appears to the creature (*as now*) and how we as investigators observe the creature (as behaving in various ways and having certain sorts of anatomical features) forges the connection between phenomenology, cognitive function, and neural structure that promises new insight into the minds of nonhuman animals and new grounds on which to make moral decisions in relation to them.

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