

Towards a Comprehensive Catalog of Zebrafish Behavior 1.0 and Beyond

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Abstract

Zebrafish (*Danio rerio*) are rapidly gaining popularity in translational neuroscience and behavioral research. Physiological similarity to mammals, ease of genetic manipulations, sensitivity to pharmacological and genetic factors, robust behavior, low cost, and potential for high-throughput screening contribute to the growing utility of zebrafish models in this field. Understanding zebrafish behavioral phenotypes provides important insights into neural pathways, physiological biomarkers, and genetic underpinnings of normal and pathological brain function. Novel zebrafish paradigms continue to appear with an encouraging pace, thus necessitating a consistent terminology and improved understanding of the behavioral repertoire. What can zebrafish 'do', and how does their altered brain function translate into behavioral actions? To help address these questions, we have developed a detailed catalog of zebrafish behaviors (Zebrafish Behavior Catalog, ZBC) that covers both larval and adult models. Representing a beginning of creating a more comprehensive ethogram of zebrafish behavior, this effort will improve interpretation of published findings, foster cross-species behavioral modeling, and encourage new groups to apply zebrafish neurobehavioral paradigms in their research. In addition, this glossary creates a framework for developing a zebrafish neurobehavioral ontology, ultimately to become part of a unified animal neurobehavioral ontology, which collectively will contribute to better integration of biological data within and across species.

Introduction

EXPANDING THE SPECTRUM of model organisms and creating a comprehensive catalog of behavioral phenotypes are

important strategies in translational neuroscience research.¹⁻³ Zebrafish (*Danio rerio*) are rapidly emerging as a useful species for studying normal or pathological behaviors⁴⁻¹⁰ and modeling complex brain disorders¹¹⁻¹⁷ (Table 1). The

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zebrafish genome is fully characterized, and their physiology and neuroanatomy parallel those of humans.^{18–21} Zebrafish breed in large numbers, are inexpensive, small and easy to manipulate genetically or pharmacologically.^{22–27} Zebrafish behavioral responses are robust, appear to be evolutionarily conserved, and resemble those of mammalian species.^{28–33} Finally, they have significant potential for high-throughput screening due to powerful video-tracking tools developed for both larval and adult zebrafish.^{25,34–36}

However, as a novel model species, the zebrafish has its own challenges.¹⁷ For example, while rodent and primate behaviors have been comprehensively evaluated and defined,^{37–41} zebrafish behavioral terminology is far less developed and consistent (see further). As Edwin Land famously noted, “a problem well defined is half solved”. Recognizing the importance of detailed and standardized terminology in behavioral research, this article presents the first catalog of zebrafish behaviors, also outlining future strategic goals and potential of its application in biomedicine.

The current glossary (Zebrafish Behavioral Catalog, ZBC) is expected to help improve the interpretation of zebrafish literature, promote cross-species behavioral modeling, and encourage more groups to employ zebrafish neurobehavioral paradigms for their research. Most of the 190 ZBC terms listed here refer to a descriptive (phenotype-based) aspect of zebrafish behavior, while others briefly mention the function of the behavior as well. The terms for this catalog were selected to the best of our knowledge, aiming to be comprehensive, cover all major behavioral domains, and target (in a balanced manner) both *adult* and *larval* zebrafish models. Future work will be needed to include in this glossary higher-level terms that focus on behavioral processes and interpretation/function of zebrafish behavior (such as learning, memory, acquisition, recall, and a large spectrum of addiction-related behavioral phenomena). However, as the first attempt to consolidate zebrafish behaviors in a single organized resource, this catalog can already serve as a tool for zebrafish investigators. Representing the intellectual consensus of multiple active zebrafish laboratories worldwide, the terminology developed in the version 1.0 of this glossary can be recommended for use by other groups working with zebrafish models.

As our understanding of zebrafish behaviors continues to grow, the ZBC glossary may undergo regular revisions and

updates, adding new behavioral phenotypes and related terms. Gradually becoming a universal reference guide for specialized zebrafish literature, such efforts will address the increasing demand for improved and standardized neurophenotyping in this rapidly expanding field.

Glossary

This section contains the alphabetized glossary of zebrafish behaviors (phenotypes) relevant to several key behavioral domains (Table 1) in adult and larval zebrafish. One of the existing challenges in the field is the nonstandardized terminology, when similar phenotypes have different meanings (e.g., circling as part of courtship⁴² vs. seizure-like behavior⁴³). Providing necessary distinctions and contexts in such cases is important, better explaining phenomenological and semantic differences which otherwise may be unclear (e.g., to nonspecialists or non-native speakers). Another problem is using various terms in a laboratory-specific manner, when different terms describe the same phenomena or behaviors (e.g., jumping, leaping, or darting for erratic movements^{29,44,45}). Therefore, detailed explanations of terms, relevant contexts and synonyms are also needed to develop the uniform terminology for zebrafish neurobehavioral research. Furthermore, several zebrafish behaviors may have similar or overlapping behavioral manifestations, with very fine (but essential and describable) differences. For example, vertical drift and sliding describe passive swimming, but in different directions (vertical vs. lateral, see glossary), whereas coasting and creeping both represent passive slow sliding, but with or without use of fins, respectively. Likewise, stress-related freezing (lack of body movements except for eyes, with increased opercular movements) can be differentiated from sleep-like/resting behavior (lack of body movement with reduced opercular activity, see glossary). Importantly, all phenotypes included here were generated by multiple active zebrafish laboratories working with both larval and adult models. While some other groups may use alternative working definitions and terms, this catalog represents a formalized consensus that can be used for standardizing terminology in this field. For this, references to published literature were provided to support the definitions and terms used in this glossary (note, however, that for some broader terms the relevant citations were provided for the individual entries, to avoid redundancy). In addition to synonyms, specific contexts (e.g., sexual, exploratory) were given for terms covering multiple distinct domains (e.g., approach, circling, swimming). Moreover, while many behaviors are relatively similar between adult and larval zebrafish models, there are some notable differences as well.^{10,32,46} which have been reflected in the glossary. Where appropriate, behavioral indices were also given as examples of measurable endpoints for the terms listed in this glossary (for more details on specific endpoints and protocols, see Refs. 47–49). For convenience, the terms provided here were numbered from 1.1 to 1.190, with 1.0 referring to the current, first version of the ZBC glossary. Citing specific behaviors in the text of research articles, referring to their respective ZBC numbers (e.g., “...recording freezing behavior (ZBC term 1.68), erratic movements (ZBC term 1.51), and vertical drifting (ZBC term 1.184)...”) may enable a better characterization and interpretation of behaviors assessed in various studies and across various laboratories. Subsequent

TABLE 1. MAJOR BEHAVIORAL DOMAINS PRESENTED IN THE CURRENT CATALOG OF ZEBRAFISH PHENOTYPES

| <i>Behavioral domains</i> | <i>Selected references</i> |
|--|-------------------------------------|
| Anxiety/fear-related behavior | 10, 29, 31, 36, 51, 68, 70, 71, 148 |
| Cognitive behavior | 59, 73, 127, 172, 173 |
| Social behavior | 11, 13, 67, 76, 174–176 |
| Reward-related behavior | 9, 13, 26, 135–139, 168, 177 |
| Sexual behavior | 42, 77, 133 |
| Pain-related behavior | 124, 128 |
| Sensory behavior | 73, 74, 120, 178–185 |
| Sleep behavior | 122, 144, 145 |
| Neurological phenotypes | 6, 149, 150 |
| General behavior, behavioral ecology and welfare | 14, 15, 25, 118, 186, 187 |

See also Zebrafish Neurophenome Project (ZNP) Database¹⁷¹ for details and specific endpoints.

modification and development of ZBC will provide 'time-stamped' references to future versions of this glossary (e.g., terms 2.68, 3.51 in ZBC 2.0 and 3.0, respectively), also see further for discussion on ontology development and additional solutions for creating unique IDs for each zebrafish behavioral term.

Finally, while most of these behaviors can be detected and quantified by manual observations, the development of reliable high-throughput IT-based techniques enables a more thorough and objective quantification of zebrafish phenotypes.^{27,31,50–58} For example, zebrafish swimming can be quantified using video-tracking software assessing velocity, distance traveled, and time spent moving during the trial.^{11,29,36,59–65} Recently developed software tools enable automated quantification of complex zebrafish group behavior, such as shoaling.¹¹ Mounting evidence also supports the value of three-dimensional (3D) analysis of zebrafish behavior, demonstrating its high sensitivity to various experimental manipulations.^{36,56,59} Future advances in IT-based methodology will eventually enable fully automated quantification of zebrafish behaviors, thereby contributing to high-throughput, data-dense behavioral analyses best utilizing the potential of these aquatic models.

1.1. Abnormal body position: Contortion of the body (e.g., droopy tail and bending); typically has a long-term nature (unlike short-term **twitches/spasms**); caused by illness, genetic defects, toxic agents, or aging. In larval zebrafish, commonly associated with neurological phenotypes and/or neurodevelopmental abnormalities.⁶⁶

1.2. Aggregation behavior: Seeking of conspecifics based on chemical, visual or other cues; exploratory approach that then leads to **shoaling**, **schooling**, and/or **sexual aggregating behavior**, where applicable.

1.3. Aggression: Complex behaviors (including **approach**, **fin raise**, **undulating body movement**, **mouth opening behavior**, **body color change**, **biting**, **charging**, **chasing**, and **circling**) directed at conspecifics (or other objects) in adult zebrafish; may appear in the context of defending the territory (**territorial behavior**), protecting resources (e.g., females) and establishing dominance (see **Social interaction**). Related to **boldness phenotype**; can be affected by different pharmacological manipulations.⁶⁷

1.4. Akinesia: A slowness of swimming or loss of normal motor function; commonly observed in aged zebrafish or after exposure to selected compounds, such as dopamine-depleting drugs (e.g., reserpine), is often accompanied by **droopy tail**; can be assessed by a global reduction in distance traveled and/or swimming velocity (similar to **hypolocomotion**), also see **Ataxia** and **Motor incoordination**.

1.5. Alarm reaction: An adaptive escape reaction which serves as an anti-predatory response exhibited in the context of fear-inducing stimulation (e.g., chemical alarm cue or visual predator exposure).^{29,45,68} Typically characterized by increased speed of movement and rapid directional changes, a response set that is often referred to as **erratic movement** (also see **Zig-zagging**). Alarm reaction may also include **freezing** with frequent **opercular movements**, changes in **shoaling** (e.g., rapid 1–2 s decreases of shoal cohesion followed by longer-lasting, up to several minutes, increase of shoal cohesion) and **diving**.^{45,68,69}

1.6. Anxiety (anxiety-like) behavior: Complex behavior evoked by dangerous or potentially dangerous environment/

stimuli. Includes reduced exploration, and typically manifests in **geotaxis (diving)**, **thigmotaxis**, **scototaxis**, **freezing**, **opercular movements**, **body color change**, and **erratic movement (zig-zagging)**.^{31,51,60,61,70,71} Anxiolytic drugs generally reduce anxiety-like behaviors, while anxiogenic agents potentiate these responses. Zebrafish anxiety-like behavior frequently overlaps with **fear-related behavior**,^{33,51,72} and future studies are needed to better characterize these two domains.

1.7. Appetitive olfactory behavior (also see **Olfactory response**): Increased rate of swimming and distance traveled with frequent directional changes (>90° turns) that serve to sample appetitive odor plumes (e.g., L-alanine, food extract).^{73–75} Once visual contact with food is established, **approach** and **nibbling** behaviors are displayed.

1.8. Approach: Display of presence, movement towards an object. *Sexual:* Abrupt swimming movement ('present') expressed independently of any male courtship behaviors; performed by females during **courtship**.⁴² *Exploratory:* approach to the novel object (part of **boldness** phenotype), opposite of **avoidance**.^{76,77} *Appetitive:* can be part of **attraction** behavior (e.g., **food seeking**).

1.9. Ataxia: A general loss of normal body posture and/or coordination of movements (e.g., **laying on a side**, **swimming on a side**, **corkscrew swimming**); commonly observed as a result of neurotoxicity-induced **motor incoordination**, **akinesia**, **seizure behavior**, and/or **paralysis**.

1.10. Attack (attacking): Short bouts of fast swimming directed at an opponent, accompanied by the **mouth opening behavior** and **biting**;⁶⁷ part of **aggression**-related behavior (differs from **strike** behavior by the presence of physical contact between fighting fish).

1.11. Attraction: Increased time spent nearby or movement towards an object (visual) or chemical stimulus (e.g., food extract); opposite to **Avoidance**.

1.12. Avoidance: Increased movement away and/or time spent away from an object or a stimulus (e.g., predator, bright light); opposite to **Attraction**.

1.13. Background adaptation: See **Camouflage response**, **Body color change**.

1.14. Backward swimming: Albeit rarely occurring in normal zebrafish, typically represents an aberrant motor behavior observed under some circumstances, such as following exposure to selected hallucinogenic drugs (e.g., lysergic acid diethylamide, LSD^{78, 79}).

1.15. Beat-and-glide: An intermittent form of **swimming** characterized by tail beating followed by gliding; appears at ~4 dpf in larvae.⁸⁰

1.16. Bend (bending): Aberrant neurological phenotype involving swimming with the body in a laterally bent position; can be observed as part of **seizure** behavior (e.g., evoked by certain convulsant agents, such as caffeine). Short-lasting bouts of this behavior represent **twitch/spasm** behavior.⁴³

1.17. Bite (biting): Quick movement towards target, with mouth opening and closing, with physical contact. *Social:* zebrafish will often bite/nip (**nipping**) each other around the gill region or fins during 'fights'. *Predatory/food:* zebrafish can attempt to bite/consume any sufficiently small item moving through their field of vision at appropriate speeds; differs from non-aggressive **nibbling**.^{67,81}

1.18. Boldness: Behavior characterized by bold personality trait, typically manifested in increased **approach** towards novel objects (also see **Risk-taking behavior**). Usually, bolder

animals also present reduced **anxiety-like behavior**, **body color change**, and increased **exploratory activity**.^{76,77,82}

1.19. Body color change (coloration response): A general change in body pigmentation resulting in a darker or lighter appearance; can be a sign of anxiety, a natural response to lighting/environmental conditions (**camouflage response**^{83,84}), a part of social behavior (e.g., **display**, **fight** or **courtship**),⁴² as well as a result of stress/sickness, or drug-evoked dispersion (skin darkening) or aggregation (paling) of melanophores.⁸⁵ Specific drugs (e.g., alcohol, ibogaine^{86,87}) evoke robust skin darkening in adult zebrafish, while some factors (e.g., cold exposure, pathogens) can evoke paling (e.g., **sickness behavior**). Coloration response can be assessed manually (by visual inspection) or using automated (luminescence-based) tools.⁸⁷

1.20. Breeding (reproductive) behavior: See **Spawning**.

1.21. Buoyancy dysregulation: Interference with the ability to control buoyancy. Characterized by an inability to remain at a constant elevation (sometimes in vertical or inclined/titles position) without exerting physical effort via swimming; most commonly caused by problems with the swim bladder or other peripheral systems;^{88,89} often manifests as **surfacing**, **vertical drifting**, **Cartesian diver behavior**, **inclined swimming**, and **tilting**.

1.22. Burst-and-coast behavior: Darting pattern specific to larval fish not yet able to perform continuous swimming.⁹⁰ Fish move forward (burst) in a single motion and glide (coast) to a slow speed, or stop from which they burst forward again.

1.23. Burst swim (swimming): Fast forward swim with large bend angles, maximally at mid-body of larval zebrafish, appears at 2 dpf in larvae. Includes larger amplitude bending (large bend angles), faster speeds and greater yaw than during slow **swimming**; often associated with **escape** behaviors; pectoral fins are tucked against the body and not active^{80,91,92}.

1.24. C-start (C-bend/turn, Mauthner reflex): Quick **escape/startle response** in which the fish body first curves to form a C-shape, and then the fish propels itself away at an angle from its previous position using a fast swim.^{93,94} Exhibited by both adult and larval fish, and is regulated by Mauthner cells (also see **O-bend** and **S-start/bend**). In larval zebrafish, head stimulation generally elicits C-starts, while tail stimulation evokes both C- and S-starts.⁹⁴

1.25. Cannibalism: Eating of dead or alive conspecifics (also see **Infanticide**, including egg cannibalism⁹⁵).

1.26. Camouflage response (background adaptation), also see: **Body color change**. A change in body pigmentation (resulting in a darker or lighter appearance) after being exposed to a darker or lighter background, respectively. Occurs due to melanophore dispersion (skin darkening) or aggregation (paling).^{83,84,86} Part of **body color change** response; in fish phenotyping literature represents 'expanded melanophore phenotype' (e.g., lack of body color change may indicate deficits in light perception, leaving the larva in a dark adapted pigmentation state).

1.27. Cartesian diver behavior: An aberrant phenotype that involves alternating between passive **vertical drift** and **sinking**; induced in fish by some neuroactive substances, such as LSD.⁷⁹

1.28. Charge (charging): Movement towards a second fish, increasing acceleration, while second fish avoids the first. Establishes social dominance, and marks the resolution of a zebrafish '**fight**'.⁶⁷

1.29. Chase (chasing): See **Charge**.

1.30. Chemotaxis (chemoattraction): Movement to/preference towards specific chemical cues serving as chemo-attractants for zebrafish. Chemically-mediated **attraction** behaviors are diverse and include **appetitive olfactory behavior** (elicited by L-alanine, food extract and others), chemically mediated **kin recognition** and **sexual aggregating behavior** (elicited by sex pheromones).^{73-75,96,97} Usually characterized by higher speed as fish follow the increasing concentrations of chemoattractants and by slower speed when fish locate the signal source.

1.31. Chewing: While lacking an upper pharyngeal jaw, zebrafish can chew their food by grinding the teeth in their lower jaw against a chewing pad on the base of the skull.

1.32. Circling (cycling, rotation): Repetitive swimming in a circular direction (usually seen during seizures, neurological impairments, and following the selected drugs' action). Normal behaviors with circling include **display**⁶⁷ (circling plays a part in lateral display behavior) and **courtship** (circling can be seen in sexual behavior);²⁸ can be quantified manually or using automated video-tracking tools. Characteristic '**tight**' circling evoked by some treatments (e.g., glutamatergic antagonists) can be defined by their diameter, expressed in body length (e.g., two body lengths/~5 cm). Commonly used circling endpoints include the number of complete circles (360°) per trial, the number (%) of animals showing circles, and the direction of circling (left- or right-rotations);^{2,98} automated methods may also quantify turn angle and angular velocity.

1.33. Coast (coasting): Passive **sliding** without body/fin movements (i.e., after the fish stopped swimming actively),⁹⁹ similar to **drifting** (also see **Creeping**, which involves slow swimming with only pectoral fin use).

1.34. Coil (coiling): Embryonic movement describing a full body contraction that brings the tip of the tail to the head (coils); can be spontaneous or evoked by touch.^{100,101} Involves single or alternating left-right bending of entire body; appears in embryo around 18 hpf, then gradually decreases in frequency.^{46,101}

1.35. Color preference: A natural preference/bias towards specific colors. For example, zebrafish will remain near some 'preferred' colors and keep away from those that induce an innate aversion (e.g., preferring black (**scototaxis**), or yellow, green, or red vs. blue¹⁰²), most likely associated with colors of natural threats, such as predators (this, however, may depend on context).⁴⁶ The color of fish objects is also an important factor in **social interaction** (e.g., **shoaling** formation) in adult zebrafish.

1.36. Coloration response: See **Body color change**.

1.37. Corkscrew swimming (spiraling, whirling): Spiral swimming with an increased speed and in an uncoordinated direction; commonly observed as part of seizure phenotype.^{43,103}

1.38. Courtship: Complex patterned behaviors that precede spawning.⁴² The male will **follow** or **chase** the female in a jerky swimming motion with his dorsal fin erect (**fin raise**), and attempt to **tail-nose touch** (this happens after the male makes visual contact, since first needs to chemically sense the readiness of female and display **sexual aggregating behavior**). If an immediate **spawning** attempt fails, the male may position himself just above the substrate with his body slightly angled downwards, and then will often display either **circling** (sometimes circling the female) or **zig-zagging**. The male will continually attempt to spawn with the female during this time. The female may **approach**, **escort**, **present**, and/

or **lead**.⁴² If the male's advance is unwelcome, the female may **chase** the male away. Zebrafish courtship behavior can be quantified manually or using automated video-tracking systems, and characterized by the following endpoints: average distance between male and female; the number of contacts between male and female; time spent in spawning area by male and female; the number of entrances into spawning area by male and female; swimming distance and velocity inside and outside spawning area; total swimming activity and turning rate by male and female.

1.39. Creeping: Very slow **swimming** during which only the pectoral fins propel the fish forward;⁴⁴ also see **coasting/drift** (passive **sliding** without fin use).

1.40. Cycling: See **Circling**.

1.41. Dart (darting): A single fast acceleration in one direction (e.g., as part of **escape** behavior) with the use of caudal fin. May be part of **dashing** or **erratic movement/zig-zagging** (associated with multiple darts, representing fast acceleration bouts in rapid succession, in which the direction of movement also changes in a seemingly stochastic manner between the darts³⁶). In some publications, darting was called **leaping** or **jumping**¹⁰⁴ (which are presently defined in ZBC as separate, distinct behavior).

1.42. Dashing: A series of directed (propulsive) **darting** movements; commonly seen as an **escape response**.

1.43. Depth preference: Natural tendency to prefer depth over shallow water⁶⁰ (note, however, that shallow water can trigger **breeding behavior**).

1.44. Dispersion: Rapid escape-like behaviors of multiple fish moving away from each other, before reuniting with the group; typically caused by the sudden exposure to a large (potentially dangerous) moving object, such as predator (also see **Shoaling**).

1.45. Display: Agonistic social behavior used to establish dominance/hierarchy, plays a role in **fighting behavior**.²⁸

Lateral display: Two fish line up parallel to each other head to tail, raise their dorsal fins (**fin raise**), extend their caudal fins, darken in color (**body color change**), and swim in circles (**circling**), often ascending. **Frontal display:** Two fish **approach** each other from the front with the attempt of **nipping/biting**.⁸¹

1.46. Dive (diving, geotaxis): Movement to/preference towards the bottom of the tank, often in response to threat.^{4,52,59,61} Generally, a very sensitive measure of **anxiety/avoidance** behavior; can be quantified by latency to bottom, time in bottom, frequency of visits to the bottom, distance traveled in bottom, and also expressed as respective top:bottom ratios. Is commonly reduced during **habituation** or anxiolytic treatments, increased by sedative/anxiogenic drugs, and can be atypically reversed by some hallucinogenic drugs (e.g., ibogaine⁸⁷). Diving is an active, fast and *directed* zebrafish behavior (with body heading towards the bottom head first); differs from passive, more slow and undirected behaviors, such as **sinking** or **Cartesian diver behavior** (typically occurring in horizontal body position), or **resting behavior**.

1.47. Dorsal light reflex (DLR): A tilting of the body axis toward a light source, commonly observed in teleost fishes.^{105,106} Briefly, illuminated horizontally, the fish inclines its dorso-ventral axis and turns dorsal surface toward the light source, with its body tilt corrected antagonistically by the vestibular righting reflex (i.e., the body inclination increases with the illumination intensity but decreases with the gravity).¹⁰⁶

1.48. Drift (drifting): See **Sliding, Coasting**.

1.49. Droopy (drooping) tail: Motor phenotype associated with neurological deficits, **akinesia**, and global **hypolocomotion**. Can be evoked by aging, motor impairments or genetic and pharmacological modulations (e.g., exposure to monoamine-depleting agent reserpine; Kalueff et al., 2011–2012, unpublished observations); extreme phenotypes may result in **inclined swimming**. Droopy tail is a long-lasting phenotype, and differs from **tail dip** (a short episode of **submissive behavior**); can also be part of a normal **resting/sleep behavior**.¹⁰⁷

1.50. Epilepsy-like behavior: See **Seizure behavior**.

1.51. Erratic movement (erratic swimming/locomotion): Complex behavior characterized by sharp changes in direction or velocity and repeated rapid **darting**; Commonly observed in adult zebrafish,^{29,108} erratic movement is associated with multiple darts (fast acceleration bouts in rapid succession in which the direction of movement also changes in a seemingly stochastic manner between the rapid darts; also see **Zig-zagging**). Usually evoked by acute stressors (predator exposure, alarm cue release) or reflects a general baseline anxiety/fear state; commonly seen immediately before or after **freezing** bouts; part of the **alarm reaction**. Larval zebrafish can also display erratic movements, for example, in response to sudden change in the light.⁴⁶

1.52. Escape (startle response, tail thrash/ing): A large body angular acceleration and displacement in response to a startling stimulus.²⁴ The first stage is a bodily 'C-bend' (**C-start**), followed by a contralateral bend and **tail beat(s)**. The initial acceleration is often followed by rapid **zig-zagging** near the bottom of the tank; in some cases, escape can lead to **jumping** behavior. In larval fish, involves **fast turning** followed by **burst swimming**.^{80,91,92}

1.53. Escort (escorting): Swimming alongside a male or remaining still while being courted; performed by females during **courtship**.⁴²

1.54. Exploratory activity: A complex group of behaviors directed at exploration of novel environments. Related to, but not dependent on, locomotor activity and anxiety-related parameters (for example, the exploratory profile of zebrafish can be measured by quantifying the ratio of their activity in different horizontal sections and vertical areas of a tank).

1.55. Fast turn (turning): Escape-like turns in larval zebrafish, characterized by fast, large-angle turns that involve bending of the entire body with high angular velocity; takes 12 ms to turn head 180°, followed by a C-shaped counter-bend and vigorous swimming episode, as larvae swim away at a 90–180° angle. Associated with **escape** responses (e.g., in response to a stimulus), typically last 6–14 ms in larvae.⁹¹

1.56. Fear-like behavior: See **Anxiety-like behavior** for details. Traditional clinical view of anxiety is that it is a state or response induced by potential (but not currently present) aversive stimuli, whereas fear is in direct response to the appearance or perception of such stimuli. Therefore, anxiety is more diffuse, and fear is more cue-oriented.^{14,33,45,68,72}

Currently, it is unclear how exactly the two conditions translate into zebrafish behavior, although certain conditions (e.g., **alarm reaction**) are more relevant to fear, while others (e.g., withdrawal) seem to represent pathological anxiety-like state.

1.57. Feeding: Behaviors related to consumption of food (see **Biting, Chewing, Nibbling**); can include some specific types of food (e.g., **cannibalism, prey capture**).

1.58. Fight (fighting): Agonistic confrontation between two individuals often used to establish social dominance;⁶⁷ comprises two distinct phases: the fish first assess each other by exhibiting **display**, **biting/nipping**, **flicking**, and **circling** behaviors, which continues until the first **chase/flee** occurs. Next, the 'winner' (chaser) initiates all agonistic behaviors, while the 'loser' displays **fleeing**, **submission behavior**, or **freezing**.⁶⁷

1.59. 'Figure eight' swimming: A specific swimming pattern observed in zebrafish following selected drug treatments (e.g., nicotine or ketamine; Kalueff et al., 2010–2012, unpublished observations); can also be part of natural **courtship** behavior (when male fish swims around female with raised fins²⁸).

1.60. Fin raise (fin extension/erection): Raising the dorsal fin and/or extending the caudal fins; common in zebrafish during **aggression** and **courtship**.¹⁰⁹

1.61. Flee (fleeing), flight behavior: Accelerating movement away from another fish or stimulus.⁶⁷

1.62. Flick (flicking): A specific agonistic behavior observed when two zebrafish swim towards each other, briefly touch mouths, and then simultaneously flick away in opposite directions; can be repeatedly displayed during agonistic interactions (**fight**).

1.63. Flight behavior: See **Flee**.

1.64. Floating: Passive swimming (typically near the water surface), differs from **surfacing** (typically a more active locomotion at the water), **drifting** (typically in the middle of the water layer) or **sleep/resting** (typically near/at the bottom); can be related to neurological impairments or **buoyancy dysregulation**.

1.65. Food seeking: A common form of zebrafish **foraging** behavior. Is triggered by hunger and can be suppressed by pathogenic conditions (e.g., **sickness behavior**) or by selected psychotropic drugs acting as appetite suppressants.

1.66. Follow (following): Behavior similar to **chase**, typically a nonaggressive movement towards (after) another fish; common during **courtship** and **social interaction**.⁴²

1.67. Foraging: Searching and/or probing movements typically in response to sensory cues (e.g., **food seeking**). Chemically induced foraging is characterized by frequent displays of directional turns as animal samples turbid chemical plumes (see **Appetitive olfactory behavior**).

1.68. Freeze (freezing): A complete cessation of movement (except for gills and eyes) by the fish while at the bottom of the tank.^{29–31,61,70} Generally, a result of high stress/anxiety or part of the **submissive behavior** (e.g., submissive immobile postures⁶⁷); can be quantified by assessing the latency, frequency, duration and location of freezing. **Opercular movements** (respiration/gill movements) are usually very frequent during stress-induced freezing. Freezing behavior differs from **immobility**, which is typically not associated with increased **opercular movements**, and usually caused by toxic/sedative agents (e.g., high ethanol concentrations), during which the animals also present **hypolocomotion** and **akinesia**; can also result in **sinking**.⁶⁷

1.69. Fright: See **Escape**.

1.70. Geotaxis: See **Dive/diving**.

1.71. Jaw movements: Stereotypic non-foraging **mouth opening behavior** observed following treatment with some drugs (e.g., hallucinogenic phencyclidine, Kalueff, 2012, unpublished observations); or convulsant agents, such as domoic acid¹¹⁰).

1.72. Habituation: Tendency to show a robustly decreased response upon repeated exposure to a novel stimulus/environment. Includes inter-trial (inter-session) and intra-trial (intra-session) habituation. Over time, typically includes increased top exploration, reduced **diving**, and unaltered **erratic movements**. Zebrafish habituation can be quantified by calculating the ratios of behavioral activity during the initial vs. latest trials, or by assessing the behavioral profile of fish across the trial(s).^{4,111}

1.73. Head-butting: Single or repeated pushing head against the vertical surface (e.g., glass, rock); commonly observed during **mirror stimulation response**, during **thrashing** behavior, or as the result of action of selected psychotropic/hallucinogenic drugs (e.g., LSD or ibogaine⁸⁷).

1.74. Head shake movements: A type of seizure/tremor-like behavior, in larval zebrafish often coupled with convulsions (typical for some convulsant drugs, e.g., domoic acid¹¹⁰).

1.75. Hide (hiding): Attempt by the fish to conceal itself (e.g., under the stationary object/shelter).¹¹²

1.76. Homebase formation/behavior: The tendency to establish a key 'safe' location which the fish spends more time in and repeatedly returns to after exploring a novel environment.¹¹³ A natural form of **place preference** behavior; can be assessed by time spent, number of visits and distance traveled in homebase (vs. non-homebase) areas. May be sensitive to some pharmacological manipulations.⁸⁷

1.77. Hyperactivity: See **Hyperlocomotion**, **Hyperactivity burst**.

1.78. Hyperactivity burst: Episode of darting-like **erratic movements** with rapid turning and high velocity locomotion *within* a single behavioral bout; can be seen in both adult and larval fish, e.g., during high **anxiety** states⁵¹ or as **seizure behavior**.¹¹⁴

1.79. Hyperlocomotion (hyperactivity): Abnormally fast swimming endured for an extended period of time; typically related to psychostimulant/convulsant action or **anxiety-like behavior**.

1.80. Hypoactivity: See **Hypolocomotion**.

1.81. Hypolocomotion (hypoactivity): Abnormally slow swimming for an extended period of time; typically related to sedation, neuromotor deficits, and **akinesia**.

1.82. Immobility: A complete cessation of movement (except for gills and eyes) at the bottom of the tank;⁶⁰ differs from **freezing** and **resting** as not always associated with altered (respectively, increased or reduced) **opercular movements** (note, however, that immobility and freezing are often used as synonyms in zebrafish literature⁸⁷). Can be caused by sedative agents (such as high ethanol concentrations), during which the animals may also present **hypolocomotion**, **akinesia**, or **paralysis**.

1.83. Inclined swimming: An aberrant phenotype (swimming with an angle relative to the water surface; **tilting**), commonly induced by neuroactive/neurotoxic substances (also see **vertical swimming** and **swimming upside down**). Can be related to **droopy tail**, **buoyancy dysregulation**, and triggered by motor deficits or aging.

1.84. Infanticide: Cannibalizing eggs (egg **cannibalism**⁹⁵) or larvae/fry.

1.85. J-bend (J-turn): Fine reorientation tuning in which the larva body slightly curves (~30°), with a characteristic bend at tail.¹¹⁵

1.86. 'Jittery' swimming: A specific pattern of **swimming** characterized by multiple short 'jerky' movements with reduced smoothness of swimming trajectories; common for some seizure behavior, can be induced by selected consultants (e.g., RDX, strychnine).¹¹⁶

1.87. Jump (jumping): A specific zebrafish behavior involving jumping out of water/tank (similar to **leaping**); usually caused by anxiogenic factors, as part of **escape** behavior or **alarm reaction** (e.g., can be triggered by predator or alarm cue exposure)¹¹⁷; also see **Terrestrial jump** (note, however, that in some publications, terms 'jumping' or 'leaping' are used to describe **darting** behavior¹⁰⁴).

1.88. Kin preference: The preference for kin vs. unrelated zebrafish, absent in larvae but particularly robust in juvenile 21-dpf zebrafish; based on chemical and visual cues (see **Kin recognition**).²⁸

1.89. Kin recognition: The ability to recognize kin (from unrelated zebrafish) and seek kin based on chemical and visual cues; involves **approach** and **attraction** and will ultimately lead to increased time spent near kin (**kin preference**; also see **Social preference/recognition**).²⁸

1.90. Laying on a side: Loss of normal body posture due to **ataxia**; commonly observed as a result of sedation and/or neurotoxicity-induced motor incoordination.¹⁰⁴

1.91. Lead (leading): Returning at least three times to one location in the tank; performed by females during **courtship**.⁴²

1.92. Leap (leaping): See **Jumping**.

1.93. Lethargy: Behavioral state indicative of chronic distress and/or illness (similar to a broader term **sickness behavior**) in adult zebrafish that includes decreased locomotor activity, reduced **escape** response, atypical body coloration and staying close to the bottom, with fins (especially dorsal) typically held close to the body.¹¹⁸ Differs from social **submissive behavior** by the chronic nature and independence of social context.

1.94. Loop (looping): Distinct circular swimming behavior in larvae around a virtual point outside of the larva's body (differs from **circling**); occurs as early as 5 dpf, common in mutants with visual feedback defects.^{119,120}

1.95. Magnetic behavior: Behavioral responsivity of zebrafish (e.g., preferred spatial orientation) to the magnetic fields.¹²¹

1.96. Mauthner reflex: See **C-start/bend**.

1.97. Meander (meandering): Movement without a fixed direction or path,^{36,61} assessed as °/m; can be increased during periods of high anxiety, especially during **erratic movement**.

1.98. Mirror stimulation response: Complex behaviors evoked in fish by mirror exposure; most likely linked to aggression; typically includes **approach**, **head-butting**, **biting** (the mirror), and **chasing** (own reflection).^{67,87}

1.99. Motor incoordination: A general loss of normal coordination of body movements (e.g., **swimming on a side**, **corkscrew swimming**); commonly observed as a result of neurotoxicity or other neurological defects (also see **Akinesia**, **ataxia**).

1.100. Mouth opening behavior: Frequent mouth opening (different from **chewing** or **biting** behavior) which can be part of **aggression/attack**, **snapping** (e.g., when exposed to food odors) or a specific **stereotypic behavior** (e.g., **jaw movements**) observed following treatment with some drugs.¹¹⁰

Mouth opening rate is significantly reduced during **resting/sleep** states.¹²²

1.101. Neophobia: Avoidance of novel objects or food (e.g., food neophobia);^{4,123} can be assessed by measuring the latency and time spent/frequency of contacting the novel object.

1.102. Nip (nipping): See **Bite (biting)**.

1.103. Nibble (nibbling): Nonaggressive **biting** on an object (usually, in **food seeking** or as part of object exploration).

1.104. Nocifensive (pain-related) behavior: Pain response to noxious stimuli, often can be experimentally induced in fish by chemical, thermal, or electrical stimulation;^{124,125} characterized by increased **swimming**, **escape**, and **tail-beating** responses (phasic stimuli induce tail beating and escape, while tonic stimuli induce **rubbing**, **tail-beating**, and increased **opercular movements**). While early views questioned pain responses in fish,¹²⁶ mounting evidence indicates the presence of pain and pain-related behavior in zebrafish.^{124,125,127,128}

1.105. O-bend: Orientation movement in which the larval zebrafish body curves to change the orientation (~180°) of swimming. In contrast to **C-bend**, this response is slower and independent of Mauthner cells; commonly elicited by dark flashes.¹²⁹

1.106. Olfactory response (olfactory behavior): Complex, odorant-evoked behavioral activity (also see **Chemotaxis**). Common changes in behavior include altered swimming speed and distance traveled (**appetitive olfactory behavior**), **avoidance** (e.g., **alarm response**) and **attraction** (i.e., during **foraging**, **spawning** or **kin recognition**).^{28,74}

1.107. Opercular movements: Respiration/gill movements of zebrafish, can be visualized using slow-mode video-recording; bi-directionally modulated by various psychotropic drugs, are markedly increased during distress¹³⁰ (e.g., during stress-induced **freezing**, where opercular beat rate can serve as an additional index of anxiety) and reduced during **resting/sleep**.¹²²

1.108. Optokinetic response/reflex (OKR): Stereotyped tracking eye movements triggered by moving objects across the visual field. Has two components: a smooth **pursuit** movement following the object, and a fast saccadic movement resetting the eyes after the object has left the visual field.¹³¹

1.109. Optomotor response/reflex (OMR): Locomotion induced by a repetitive moving stimulus presentation (e.g., rotating drum), as zebrafish will generally swim in the same direction as the moving pattern.¹³²

1.110. Oscillations of locomotor activity: Sinusoidal aspect of zebrafish locomotion/swimming, with alternating high- and lower-velocity phases (usually, with the frequency of 4–5 min) when exposed to novel environments.⁶²

1.111. Oviposition: Release of eggs by the female during **spawning**.^{28,133}

1.112. Pain-related behavior: See **Nocifensive behavior**.

1.113. Parallel (paralleling): Behavior during **spawning**, when the male swims alongside the female, in contact but slightly behind it, with head approximately leveling the female's operculum.¹³³

1.114. Paralysis: A complete cessation of all movement, including eyes, gills/operculum and fins (similar to **ataxia**, but with more severe/global motor impairment, often with an abnormal posture, such as laying on the side, floating upside down or standing vertically¹⁰⁴). Usually caused by selected neuroparalyzing agents⁸⁰ or genetic neurological mutations.¹³⁴

1.115. Photokinesis (phototaxis): General movement in response to light, including *positive* (light seeking/dark avoidance, **scotophobia**) and *negative* (light avoidance, dark preference, **scototaxis**). Zebrafish display sensitivity to visible light (positive phototaxis in larval fish; light avoidance in adult fish), and negative phototaxis to ultraviolet (UV) light (**UV avoidance**).

1.116. Photomotor response (PMR): A stereotypic series of motor behaviors in embryonic zebrafish in response to light stimulation, as zebrafish show motor excitation (lasting 5–7 s) with vigorous shaking, followed by a refractory phase, during which basal locomotion is suppressed and animals do not respond to another light pulse.^{57,58}

1.117. Phototaxis: See positive and negative **photokinesis (scotophobia and scototaxis)**.

1.118. Piping: Gulping air at the water surface; can be indicative of distress (e.g., hypoxia or toxicity),¹³⁰ but may also be seen during depth-related adjustment of swim bladder volume (during **diving**).^{88,89}

1.119. Place preference: The tendency to establish a preferred location in which the fish spends more time. Can be induced by drugs (e.g., in conditioned place preference paradigms, CPP^{9,123,135–139}), repeated administration of food/food odors,⁷³ social reward,¹³ or be based on natural behaviors (e.g., **homebase formation**¹¹³) or preferences (e.g., **depth preference**, **scototaxis**, **thigmotaxis**^{31,59,60}).

1.120. Polarization: Behavioral characteristic of adult zebrafish reflecting the degree to which members of the group are moving in the same direction; is high in zebrafish schools (see **Schooling**) and reduced in shoals (see **Shoaling**).¹⁴⁰

1.121. Prey capture (capturing): A complex behavior of larval zebrafish; consists of identifying the prey (e.g., paramecium) visually or using chemosensation, tracking it with a series of **routine turns**, forward slow **swim** and/or **J-turns**, followed by capture and ingestion (**feeding behavior**).¹⁴¹ The initial bends have low amplitude and are prominent at far-caudal locations; later bends originate more rostrally, have higher amplitude and are accompanied with increased **tail-beat frequency**.^{91,142}

1.122. Predator inspection: An exploratory/**boldness**-related **risk-taking behavior** in fish associated with either increased or decreased tendency to **approach** a predator, potentially to gather information about the identity, precise location and/or current motivational state of the predator.¹⁴³ Commonly observed in fish when **shoaling**, as they leave the shoal, swim towards the predator, and then return to the group.

1.123. Predatory attack: Adult and larval zebrafish may attempt to bite/consume any sufficiently small item moving through their field of vision at appropriate speeds (see **Biting**); in larval zebrafish, develops at ~4 dpf, and manifests as **prey capture behavior**.^{91,141,142}

1.124. Present (presenting): Halting and exposing side in front of a male or swimming up and down in front of male; performed by females during courtship.⁴²

1.125. Quiver (quivering): High frequency, low amplitude tail oscillation by a male while aligned against the side of a female; occurs during **spawning**.^{28,42}

1.126. Reflection chase (chasing): A behavior that includes chasing own reflection (e.g., in the observation tank or as part of the **mirror stimulation response**);⁶⁷ can also be triggered by selected psychoactive (e.g., hallucinogenic) drugs.⁸⁷

1.127. Reproductive (breeding) behavior: see **Spawning**.

1.128. Rest behavior (resting): Sleep-related behavior in adult and larval zebrafish. Typical rest behavior in larval zebrafish includes floating with head down, or staying horizontal close to the bottom of the tank (**immobility**, **hypocomotion**).^{144,145}

1.129. Retreat (retreating): A social behavior relevant to dominance in zebrafish, generally involves a submissive fish swimming rapidly away from the opponent (e.g., from a dominant fish) in response to an **attack** (e.g., after a **strike**, **bite**, **chase**, or **charge**), part of **fleeing behavior**.⁶⁷

1.130. Rheotaxis: A common behavior in aquatic species, includes turning towards a current and a tendency to swim upstream; displayed by both larval and adult zebrafish. In experimental setting, manifests in **avoidance** by zebrafish of the sucking source (e.g., sucking pump or stand-pipe).^{146,147}

1.131. Risk-taking behavior: Propensity of zebrafish to engage in dangerous situations (part of their **boldness** phenotype);¹⁴³ commonly occurs when a prey fish approaches/inspects a predator (see **Approach**, **Predator inspection**), and/or when a shoal member leaves the group (see **Shoaling**).

1.132. Rotation behavior: See **Circling**, **Cycling**.

1.133. Routine turn(ing); R-turn(ing): A slow spontaneous turn (20–30 ms) with a large bend angle (~60°) resulting in reorientation of the larva before forward **swimming**, **prey capture**; lacks the large counter-bend (shown in **escape turns**), with only a small portion of the tail bending; has a slow angular velocity with relatively slow turning angles.⁹¹

1.134. Rub (rubbing): A characteristic aberrant zebrafish behavior involving rubbing body sides on the sides of the tank (or the surface of other objects); typically caused by pathogenic conditions (e.g., skin disease and/or parasitic infection).¹¹⁸

1.135. Scoot swim (swimming): See **Slow swim**.

1.136. Scotophobia: A natural preference for light (or avoidance of dark) lighting/environment, commonly observed in larval fish; usually is replaced with **scototaxis** in adult fish (also see **Photokinesis**).⁴⁶

1.137. Scototaxis: A natural preference for dark (or avoidance of bright) lighting/environment in adult zebrafish.^{70,71,148} Generally, a measure of anxiety (reduced by anxiolytic drugs and increased by anxiogenic agents). Note that larval zebrafish display opposite behavior (**scotophobia**). Can be quantified in the light-dark box tests (by assessing the latency, time spent in light or dark, distance traveled, the number of visits, the average duration of a visit; and by the respective behaviors' light:dark ratios); also see **Photokinesis**.

1.138. School (schooling): Formation of a relatively polarized group (school) in which multiple fish swim together, in a coordinated/synchronous fashion; part of **aggregation behavior** that increases **foraging** efficiency as well as the ability to detect and/or avoid predators. Schools may disperse into shoals (see **Shoaling**) which show **reduced polarization**.¹⁴⁰

1.139. Seizure (seizure-like/epilepsy-like) behavior: Involuntary, rapid movements of body (usually, as a result of pathology, such as epilepsy) observed in both larval and adult zebrafish; include **ataxia**, **corkscrew (spiral) swimming**, **hyperactivity**, **circling**, **spasms**, **weaving**, **head shake movements**, **tremor**, and/or **jittery locomotion**. Severe cases include death. Can be quantified manually (using seizure scale) or applying automated video-tracking tools (by assessing the velocity and distance traveled).^{110,114,149,150}

1.140. Sexual aggregating behavior: Instinctive response to chemical cues released from females during ovulation; males display **attraction**, **approach** and **courtship** behaviors once female is identified.⁴²

1.141. Shoal (shoaling): Formation of a relatively non-polarized group (shoal) of adult zebrafish, held together by social pressures (i.e., not by individual attraction to an external stimulus); part of **aggregation behavior**. Anxiety/fear causes the shoal to 'tighten' (the fish swim closer together) and potentially form a school (see **Schooling**).^{64,140,151} Hunger/habituation causes the shoal to become looser and less organized. Zebrafish shoaling has an oscillating dynamic, and this behavior can be quantified manually or using automated video-tracking systems, assessing several endpoints, including the average inter-fish distance; shoal area size; proximity (time each member of the shoal spent within a specified distance from each other); nearest and farthest neighbor distances; time spent in shoal; time spent away from shoal; number of animals leaving the shoal (also relevant to **risk-taking behavior**) and **polarization** (reflecting the uniformity of heading).

1.142. Shyness: A reduced **exploratory activity**, reduced general activity in a novel environment and/or in response to stimuli, or reduced risk-taking behavior (opposite to **boldness**).⁸²

1.143. Sink (sinking): Freezing behavior during which the fish remains immobile (except for the eyes and gills) but changes its position in the water column (moving from top to bottom) without moving any of its fins⁴⁴ (also see **Cartesian diver behavior**).

1.144. Sickness behavior: A broad cluster of behaviors indicative of illness (or pain) that include **hypoactivity**, inhibited exploration, **feeding** or **food seeking**, pale **body color**, and **lethargy** (with fins typically held close to the body).¹⁵²

1.145. Sleep (sleep-like behavior): Activity characterized in zebrafish by **rest behavior**, including reversible **immobility/hypolocomotion**, elevated arousal threshold, reduced respiratory rate (e.g., **opercular movements**) and mouth opening frequency, and a compensatory rebound in response to sleep deprivation.^{107,122,144,145,153–156} In adult zebrafish, includes brief periods of inactivity, often with a drooping caudal fin (see **Droopy tail**), alternated with active periods of **swimming**; can be easily reversed by startling stimuli, such as tapping, sound, or weak electric field.^{111,112,119–124}

1.146. Slide (sliding): See **Coasting**.

1.147. Slow swim (slow/scoot swimming): Larval zebrafish slow **swimming** (scoots) characterized by small bend angles with bend location near the tail. Maximal bending occurs close to the tail; low degree of bending and tail beat frequency; yaw angles are $< 3^\circ$; pectoral fins are active and alternate right to left between adduction and abduction.^{91,92}

1.148. Snap (snapping): Reflexive opening and closing of mouth during exposure to high concentrations of appetitive stimuli (e.g., L-alanine, food extract); signals initiation of ingestive phase during **feeding**.¹⁵⁷

1.149. Spasm (twitch, twitching): Spontaneous, rapid movements of body (usually, as a result of neurological/neurotoxic impairment, such as **seizure**)¹¹⁶.

1.150. Spatiotemporal stability: The ability to withstand changes in environmental characteristics during exploration of a novel environment, primarily by scaling locomotor ac-

tivity (e.g., distance traveled) to the size of the environment, but retaining the temporal budgeting of the activity; can be evaluated by temporal distribution of locomotion and position in a test tank (e.g., distance traveled, transitions and time spent in each area).⁶²

1.151. Social interaction: Normal social behavior of zebrafish, represents a reciprocal change in zebrafish behavior influenced by the presence or actions of other conspecifics.^{13,67,151} Some examples include **fighting/aggression**, **shoaling/schooling**, **courtship** and **spawning**; can also manifest in **approach/boldness** (social investigation), **social recognition**, and **social preference**.

1.152. Social preference: A natural tendency to spend time close to conspecifics; can be observed as part of **shoaling** behavior, **kin recognition**, **social recognition**, or preference of the 'conspecific' vs. 'empty' compartments of the tank.^{13,28}

1.153. Social recognition: The ability of zebrafish to recognize familiar from unfamiliar zebrafish.²⁸

1.154. Spiraling: See **Corkscrew swimming**, **whirling**.

1.155. Spawning (breeding/reproductive behavior): During breeding, the male zebrafish approaches the female and curves body around, positioning his genital pore next to hers (also see **Parallel**). The male then quivers in an attempt to trigger **oviposition** in the female; sperm is released simultaneously to fertilize the newly released eggs. Spawning behavior can be promoted by exposure of zebrafish to shallow water.²⁸

1.156. S-start/bend: Quick **escape/startle response** in which the fish body curves to form an S-shaped body bend with simultaneous activity rostrally on one side, and caudally on the other (also see **O-bend** and **C-start/bend**). In larval zebrafish, head stimulation generally elicits C-starts, while tail stimulation evokes both C- and S-starts.⁹⁴

1.157. Startle response: An evolutionarily conserved, adaptive behavior in response to sudden, usually aversive, stimuli (see **Escape**), such as vibration, light, sound, or touching (e.g., **touch response**);^{24,94} may involve 'C-start' behavior, during which **coiling** and **dashing** may be observed.⁹⁴

1.158. Stereotypic behaviors: A pattern of rigid, repetitive behaviors other than **swimming** (see **Stereotypic locomotion/swimming**), evoked in zebrafish under some conditions, e.g., stereotypic **mouth opening behavior** following treatment with some hallucinogenic drugs (e.g., phencyclidine; Kalueff et al., 2011–2012, unpublished observations).

1.159. Stereotypic locomotion (stereotypic swimming): A pattern of rigid, repetitive behaviors (e.g., swimming from corner to corner) evoked in zebrafish under some conditions (e.g., treatment with psychostimulants like nicotine and caffeine, or hallucinogens like ibogaine or phencyclidine^{87,98}).

1.160. Strike (striking): An **aggression**-related behavior, observed in zebrafish when the fish swims rapidly toward the opponent, but without physical contacts between them. Differs from **approach** by a generally much higher velocity and its aggressive (rather than investigatory) nature (also see **Attack**, which occurs *with* physical contact).⁶⁷

1.161. Struggle (struggling): A behavior observed in larval zebrafish, characterized by longer alternating motor bursts at lower frequencies than **swimming**. During struggling, motor bursts propagate in inverse directions along the body, compared with swimming behavior.¹⁵⁸

1.162. Submissive behavior: A social behavior following aggressive confrontations between zebrafish. Submissive fish

stays immobile (with fins retracted), typically near the bottom or near the surface of the aquaria (also see **Freezing**), with the caudal part of the body oriented downward (also see **Tail dip**, representing the initial form of submissive behavior).⁶⁷

1.163. Surface touching: See **Surfacing**.

1.164. Surfacing (surface touching): Dwelling of fish at the surface of the water; is usually evoked by selected neuroactive drugs, mainly serotonergic agonists and glutamatergic antagonists,^{79,159} may also be related to **buoyancy dysregulation**.

1.165. Swim (swimming): Simple zebrafish locomotion; can be categorized by its duration as 'prolonged,' which may be maintained for minutes, or as 'sustained,' which may be maintained for hours. In larvae, includes **slow swim** (point of maximal body bending occurs close to the tail) and **burst swim** (maximal body bending occurs near the mid-body; maintained over seconds or less, includes larger-amplitude bending, faster speed, and greater yaw (vs. slow swim), also see **Beat-and-glide**). Selected forms of aberrant swimming include **swimming on a side**, **upside down**, **vertical swimming**, **Cartesian diver behavior**.

1.166. Swimming on a side: Loss of normal body posture due to **ataxia**; commonly observed as a result of sedation and/or neurotoxicity-induced motor incoordination.

1.167. Swimming upside down: An aberrant phenotype (swimming in an upside down position), commonly induced by neuroactive/neurotoxic substances;¹⁰⁴ also see **Inclined** and **Vertical swimming**.

1.168. Tail dip (tail dipping): An agonistic behavior during **fighting**, when one fish slightly drops its tail for a short period of time, to signal its submission and end the confrontation¹⁶⁰ (differs from **droopy tail**, which a long-lasting behavior; see **Submissive behavior**).

1.169. Tail beat (beating, slapping): Characterized by repeating episodes of rhythmic, rostral-caudally progressing peripheral nerve discharges that are alternated between the two sides of the body. Viewed from above, tail beating is physically apparent in side-to-side sweeping of the tail (that can be measured as tail beat amplitude).

1.170. Tail-nose touch(ing): Touching the side or tail of another fish with the nose or head. Performed by males during **social interaction**, especially **courtship**.⁴²

1.171. Terrestrial jump(ing): A coordinated **leap** (using tail-flip) in response to placement on a damp surface (e.g., after **jumping** out of water); can be quantified by amplitude (height) and frequency of the leaps.¹⁶¹

1.172. Territorial behavior: Monopolization and aggressive defense of a defined area in a habitat/tank¹⁶² (e.g., **spawning** sites are a commonly defended territory in zebrafish). Trespassers into the territory may be chased or bitten by the dominant fish, or can '**fight**' to challenge its dominance.

1.173. Thigmotaxis: A preference for staying in close proximity to the edge/side (and avoiding the central open areas); generally, can serve as a measure of zebrafish anxiety.^{31,51,60}

1.174. Thrashing: Forceful swimming with the use of the caudal fin while physically in contact with the side or bottom wall of the tank; swimming against the glass wall of the tank that appears as if the fish is trying to swim through the glass barrier.⁴⁴ This behavior can be thrashing *towards* an appetitive cue (e.g., food) or thrashing *away* from an aversive stimulus (e.g., representing an **escape**); can be similar to **head-butting** behavior (e.g., during the mirror stimulation test).

1.175. Tilt (tilting): Deviation from the horizontal position;⁴⁴ is often seen during **inclined swimming**.

1.176. Top dwelling: Dwelling in the top half of the tank; can include aberrant swimming very close to water surface (**surfacing**).

1.177. Touch response: Startle behavior-related phenotype evoked by the touch in an embryo, which responds with fast **coiling** of the trunk bending over the head; appears around 21 hpf.¹⁰⁰

1.178. Trance-like swim(ming): A slow swimming motion induced in fish by specific psychotropic drugs (e.g., chronic fluoxetine or hallucinogens, such as LSD⁷⁹ or salvinorin A¹³⁹); often includes a swimming pattern characterized by a slow (albeit active) bout of horizontal swimming for 1–2 s, followed by a similarly short passive gliding motion.

1.179. Tremor behavior: Specific shivering-like behavior, most typically evoked in adult or larval zebrafish by selected neurotoxic/convulsant drugs, such as domoic acid (also see **Seizures** and **Weaving**);¹¹⁰ particularly visible in the tail area.

1.180. Turn (turning): A simple change in swimming direction observed in both adult^{36,61} or larval⁹¹ zebrafish. Larval zebrafish show several specific forms of turning behavior, including **slow routine turns** (lacking the large counterbend of escape turns) and **fast turns** (fast, large angle turns characteristic of **escape** responses).⁹¹

1.181. Twitch (twitching): See **Spasm**.

1.182. Undulating body movement: A wave-like or snake-like motion; part of **aggression**-related behaviors,¹⁰⁹ and occurs mainly at the beginning of the **fight**, especially between two equal opponents. This behavior is common in fish species, and is likely related to the use of lateral line by fish to size-up the opponent by the waves generated by its movement. Although less visible in zebrafish (compared to other fishes), their undulating body movement can be observed using high-resolution videos (sometimes this behavior is followed by forceful **tail beats**).¹⁰⁹

1.183. UV avoidance: Avoidance of UV light (negative **photokinesis/phototaxis**) reported in zebrafish larvae as early as 4 dpf.¹⁶³

1.184. Vertical drift (drifting): An aberrant phenotype that involves passive floating vertically (i.e., passive vertical motion from bottom to top);¹⁶⁴ commonly induced by neuroactive/neurotoxic substances or agents related to **buoyancy dysregulation** (also see **Vertical swimming**); opposite to **sinking** (also see **Cartesian diver behavior**).

1.185. Vertical swim (swimming): An aberrant fish phenotype that involves swimming vertically (typically heads up at the surface);⁷⁹ commonly induced by neuroactive (e.g., LSD) or neurotoxic substances, or agents related to **buoyancy dysregulation** (also see **Inclined swimming** and **Swimming upside down**).

1.186. Vestibulo-ocular reflex (VOR): Compensatory eye movements in zebrafish in response to linear/angular acceleration as well as changes in head position with respect to gravity, in order to stabilize the retinal image.^{165,166} These movements are evoked through the semicircular canals of the vestibular apparatus in zebrafish.

1.187. Weaver (weaving): Aberrant tremor/shaking-like phenotype, typically evoked by selected neurotoxic/convulsant agents (e.g., strychnine; Kalueff et al., 2011–2012,

unpublished observations); similar to **tremor** and **head shake movements** (also see **Seizure behavior**).⁴³

1.188. Whirl (whirling): See **Corkscrew swimming, spiraling**.

1.189. Withdrawal-related behavior: A characteristic behavioral syndrome observed in zebrafish following discontinuation of drugs of abuse (e.g., ethanol, morphine); typically characterized by elevated **anxiety/fear-like behavior**.^{167,168}

1.190. Zig-zagging (zigzagging): *Sexual:* a tail sweep and circle along a female's body resembling a 'figure eight'; typically performed by males during **courtship**.⁴² *Stress-induced:* **erratic movement** with multiple **darts**, during which the direction of movement changes in a seemingly alternating (zig-zag-like) manner between the darts.^{45,51}

Conclusion

Overall, the terminology developed here represents an updated and standardized catalog of multiple zebrafish behavioral phenotypes. Its primary goal is to enable a better understanding of fish behavior, thereby enhancing zebrafish-based neuroscience research. There are several additional potential applications of this catalog, including fostering further translational cross-species behavioral modeling; de-

veloping novel models using zebrafish (and other fish species); providing a starting point for training investigators and students working with zebrafish behavioral tests; and encouraging new groups to actively adopt zebrafish neurobehavioral paradigms for their research.

Representing a community-driven neurophenotyping effort initiated by the International Zebrafish Neuroscience Research Consortium (ZNRC) and the Zebrafish Neuropenome Project (ZNP),¹⁶⁹ this catalog can eventually lead to the development of comprehensive ethogram of zebrafish behaviors. It can also contribute to the development of a zebrafish neurobehavioral ontology (ZNBO), in which the outlined behaviors (phenotypes) will be integrated with other biological categories and phenomena. As shown in Figure 1, individual zebrafish behaviors presented here (e.g., freezing, shoaling) can be further connected into a large-scale dynamic network, which can include 'vertical links' to larger semantic units, such as 'behavioral domains' (e.g., affective, social; Table 1), brain disorders or syndromes associated with them (e.g., anxiety/fear, autism), or developmental stages (e.g., adult vs. larval zebrafish). This network may also include multiple relevant 'horizontal' links, such as physiological biomarkers/correlates (e.g., specific endocrine or neurochemical responses), environmental modifiers (e.g., genetic

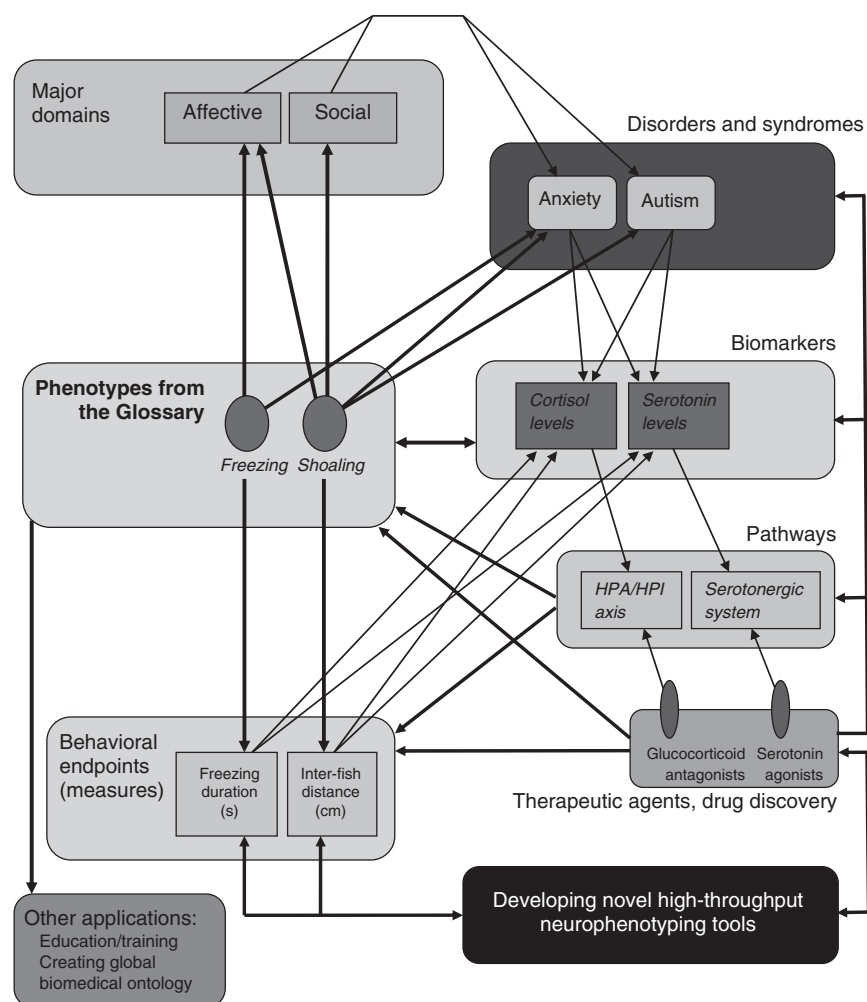


FIG. 1. Potential for further integration of zebrafish behavioral phenotypes with other biological phenomena and related processes.

mutations or pharmacological treatments), as well as top-down links to smaller semantic units, such as individual behavioral endpoints/indices (e.g., no-mobility duration during freezing or average inter-fish distance in fish shoals; Fig. 1) used to quantify various zebrafish phenotypes.

Although an important initiative *per se*, the proposed ZNBO can be joined with other biological ontologies. For example, it can contribute to the existing zebrafish ontologies within the Zebrafish Information Network (ZFIN) Project,¹⁷⁰ which currently does not contain behavioral data. Collaborative efforts are currently underway to achieve this goal. Likewise, ZNBO can be a valuable addition to the growing Animal Behavior Ontology (ABO) and Neurobehavior Ontology (NBO), eventually becoming part of the global biological ontology. NBO currently consists of two main components (an ontology of behavioral phenotypes and an ontology of behavioral processes), but lacks zebrafish data. Therefore, the present catalog of zebrafish phenotypes may become a useful addition to the first component of NBO, while future efforts (expanding this glossary to include behavioral processes) can be federated with the second component of NBO. Furthermore, while references to the ZBC term ID numbers (e.g., ZBC term 1.28 for *charging*, ZBC term 1.67 for *foraging*) offers one way of improved characterization and presenting of specific behaviors assessed in various studies from different laboratories, ZNRC is currently establishing collaborations with expert ontologists, to assign each catalogue term a unique 'bio-ontology' ID (which will then be easily searchable and compatible across ZBC as well as ZFIN, NBO, and multiple other existing biological ontologies). Collectively, these efforts will foster better and more global integration of behavioral data within and across species, including human behavior-related disease phenotypes.

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Disclosure Statement

No competing financial interests exist.

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