

## **‘Cognitive control of escape behaviour’ – Supplemental references**

*Dominic A. Evans, A. Vanessa Stempel, Ruben Vale, Tiago Branco*

*Listed below are additional references that supplement those already cited in the main text; references are grouped according to general topic areas covered in the review, as indicated by the headings. Reviews are marked with an asterisk.*

### **Threat detection**

#### *Circuits specialised to detect kairomones in vertebrates and invertebrates*

- Papes, F. et al. (2010) The Vomeronasal Organ Mediates Interspecies Defensive Behaviors through Detection of Protein Pheromone Homologs. *Cell* 141, 692–703
- Martinez, R.C. et al. (2011) Amygdalar roles during exposure to a live predator and to a predator-associated context. *Neuroscience* 172, 314–328
- Ferrero, D.M. et al. (2011) Detection and avoidance of a carnivore odor by prey. *Proc. Natl. Acad. Sci.* 108, 11235–11240
- Ebrahim, S.A.M. et al. (2015) Drosophila Avoids Parasitoids by Sensing Their Semiochemicals via a Dedicated Olfactory Circuit. *PLoS Biol.* 13, 1–18
- Carvalho, V.M.A. et al. (2015) Lack of spatial segregation in the representation of pheromones and kairomones in the mouse medial amygdala. *Front. Neurosci.* 9, 283
- Liu, Z. et al. (2018) Predator-secreted sulfolipids induce defensive responses in *C. elegans*. *Nat. Commun.* 9:1128

#### *Collision-detecting circuits and looming-sensitive cells across species*

- Schlotterer, G.R. (1977) Response of the locust descending movement detector neuron to rapidly approaching and withdrawing visual stimuli. *Can. J. Zool.* 55, 1372–1376
- King, J.G. et al. (1999) Selective, unilateral, reversible loss of behavioral responses to looming stimuli after injection of tetrodotoxin or cadmium chloride into the frog optic nerve. *Brain Res.* 841, 20–26
- Gabbiani, F. et al. (2002) Multiplicative computation in a visual neuron sensitive to looming. *Nature* 420, 320–324
- Gahtan, E. et al. (2002) Evidence for a Widespread Brain Stem Escape Network in Larval Zebrafish. *J. Neurophysiol.* 87, 608–614
- Wu, L.Q. et al. (2005) Tectal neurons signal impending collision of looming objects in the pigeon. *Eur. J. Neurosci.* 22, 2325–2331
- Fotowat, H. et al. (2009) A Novel Neuronal Pathway for Visually Guided Escape in *Drosophila melanogaster*. *J. Neurophysiol.* 102, 875–885
- Münch, T.A. et al. (2009) Approach sensitivity in the retina processed by a multifunctional neural circuit. *Nat. Neurosci.* 12, 1308–1316
- Cohen, J.D. and Castro-Alamancos, M.A. (2010) Neural Correlates of Active Avoidance Behavior in Superior Colliculus. *J. Neurosci.* 30, 8502–8511
- Billington, J. et al. (2010) Neural processing of imminent collision in humans. *Proc. R. Soc.* 278, 1476–1481.
- Nakagawa, H. and Hongjian, K. (2011) Collision-Sensitive Neurons in the Optic Tectum of the Bullfrog, *Rana catesbeiana*. *J. Neurophysiol.* 104, 2487–2499
- Carbone, J. et al. (2018) Characterization and modelling of looming-sensitive neurons in the crab *Neohelice*. *J. Comp. Physiol.* 204, 487–503
- Dewell, R.B. and Gabbiani, F. (2018) Biophysics of object segmentation in a collision-detecting neuron. *eLife.* 7, e34238
- Dewell, R.B. and Gabbiani, F. (2018) M-current regulates firing mode and spike reliability in a collision-detecting neuron. *J. Neurophysiol.* 120, 1753–1764

### **Neural activity manipulations that elicit or modify defensive behaviours**

- Hunsperger, R.W. (1956) Role of substantia grisea centralis mesencephali in electrically-induced rage reactions. *Prog. Neurobiol.* 2, 289–294
- Olds, M. and Olds, J. (1962) Approach-escape interactions in rat brain. *Am. J. Physiol.* 203, 803–810
- Halpern, M. (1968) Effects of midbrain central gray matter lesions on escape-avoidance behavior in rats. *Physiol. Behav.* 3, 171–178
- Nashold, B.J. et al. (1969) Sensations evoked by stimulation in the midbrain of man. *J. Neurosurg.* 30, 14–24
- Cools, A.R. et al. (1983) Picrotoxin microinjections into the brain: a model of abrupt withdrawal “jumping” behaviour in rats not exposed to any opiate? *Eur. J. Pharmacol.* 90, 237–243
- Cools, A.R. et al. (1984) The striato-nigro-collicular pathway and explosive running behaviour: functional interaction between neostriatal dopamine and collicular GABA. *Eur. J. Pharmacol.* 100, 71–77
- Sahibzada, N. et al. (1986) Movements Resembling Orientation or Avoidance Elicited by Electrical Stimulation of the Superior Colliculus in Rats. *J. Neurosci.* 6, 723–733

- Dean, P. et al. (1988) Responses resembling defensive behaviour produced by microinjection of glutamate into superior colliculus of rats. *Neuroscience* 24, 501–510
- Bandler, R. and Carrive, P. (1988) Integrated defence reaction elicited by excitatory amino acid microinjection in the midbrain periaqueductal grey region of the unrestrained cat. *Brain Res.* 439, 95–106.
- Northmore, D.P.M. et al. (1988) Behavior evoked by electrical stimulation of the hamster superior colliculus. *Exp. Brain Res.* 73, 595–605
- Sudré, E.C.M. et al. (1993) Thresholds of electrically induced defence reaction of the rat: Short- and long-term adaptation mechanisms. *Behav. Brain Res.* 58, 141–154
- Behbehani, M.M. (1995) Functional characteristics of the midbrain periaqueductal gray. *Prog. Neurobiol.* 46, 575–605
- De Oca, B.M. et al. (1998) Distinct regions of the periaqueductal gray are involved in the acquisition and expression of defensive responses. *J. Neurosci.* 18, 3426–3432
- Vianna, D.M.L. et al. (2001) Lesion of the Ventral Periaqueductal Gray Reduces Conditioned Fear but Does Not Change Freezing Induced by Stimulation of the Dorsal Periaqueductal Gray. *Learn. Mem.* 8, 164–169
- DesJardin, J.T. et al. (2013) Defense-Like Behaviors Evoked by Pharmacological Disinhibition of the Superior Colliculus in the Primate. *J. Neurosci.* 33, 150–155
- Liang, F. et al. (2015) Sensory Cortical Control of a Visually Induced Arrest Behavior via Corticotectal Projections. *Neuron* 86, 755–767
- Assareh, N. et al. (2016) The Organization of Defensive Behavior Elicited by Optogenetic Excitation of Rat Lateral or Ventrolateral Periaqueductal Gray. *Behav. Neurosci.* 130, 406–414

### **Previous predator encounters modify threat perception and escape**

#### ***Behavioural data***

- Melzack, R. (1961) On the Survival of Mallard Ducks after “Habituation” to the Hawk-Shaped Figure. *Behaviour* 17, 9–16
- Dill, L.M. (1974) The escape response of the zebra danio (*Brachydanio rerio*) II. The effect of experience. *Anim. Behav.* 22, 723–730
- Engel, J.E. and Hoy, R.R. (1999) Experience-dependent modification of ultrasound auditory processing in a cricket escape response. *J. Exp. Biol.* 202, 2797–2806
- Hazlett, B.A. (2003) Predator Recognition and Learned Irrelevance in the Crayfish *Orconectes virilis*. *Ethology* 109, 765–780
- Ferrari, M.C.O. et al. (2005) The role of learning in the development of threat-sensitive predator avoidance by fathead minnows. *Anim. Behav.* 70, 777–784
- Crook, R.J. et al. (2011) Peripheral injury induces long-term sensitization of defensive responses to visual and tactile stimuli in the squid *Loligo pealeii*, Lesueur 1821. *J. Exp. Biol.* 214, 3173–3185
- Crook, R.J. et al. (2014) Nociceptive sensitization reduces predation risk. *Curr. Biol.* 24, 1121–1125
- Chivers, D.P. et al. (2014) Background level of risk determines how prey categorize predators and non-predators. *Proc. R. Soc. B Biol. Sci.* 281, 20140355.
- Hegab, I.M. et al. (2014) The ethological relevance of predator odors to induce changes in prey species. *Acta Ethol.* 18, 1–9
- Brown, G.E. et al. (2015) Background risk and recent experience influences retention of neophobic responses to predators. *Behav. Ecol. Sociobiol.* 69, 737–745
- Collier, A. and Hodgson, J.Y.S. (2017) A Shift in Escape Strategy by Grasshopper Prey in Response to Repeated Pursuit. *Southeast. Nat.* 16, 503–515
- Nordell, C.J. et al. (2017) Flight initiation by Ferruginous Hawks depends on disturbance type, experience, and the anthropogenic landscape. *PLoS One* 12, 1–17
- Seehafer, K. et al. (2018) Ontogenetic and experience-dependent changes in defensive behavior in captive-bred Hawaiian bobtail squid, *Euprymna scolopes*. *Front. Physiol.* 9, 1–10
- Park, C. et al. (2018) Effects of Social Experience on the Habituation Rate of Zebrafish Startle Escape Response: Empirical and Computational Analyses. *Front. Neural Circuits* 12, 1–16
- Fanselow, M.S. (2018) The role of learning in threat imminence and defensive behaviors. *Curr. Opin. Behav. Sci.* 24, 44–49 \*

#### ***Neural correlates and mechanisms***

- Holmqvist, M.H. and Srinivasan, M. V. (1991) A visually evoked escape response of the housefly. *J. Comp. Physiol. A* 169, 451–459
- Engel, J.E. and Hoy, R.R. (1999) Experience-dependent modification of ultrasound auditory processing in a cricket escape response. *J. Exp. Biol.* 202, 2797–2806
- Yamamoto, K. et al. (2003) Input and Output Characteristics of Collision Avoidance Behavior in the Frog *Rana catesbeiana*. *Brain. Behav. Evol.* 62, 201–211
- Matheson, T. (2003) Plasticity in the Visual System Is Correlated With a Change in Lifestyle of Solitary and Gregarious Locusts. *J. Neurophysiol.* 91, 1–12
- Gray, J.R. (2005) Habituated visual neurons in locusts remain sensitive to novel looming objects. *J. Exp. Biol.* 208, 2515–2532
- Fotowat, H. et al. (2009) A Novel Neuronal Pathway for Visually Guided Escape in *Drosophila melanogaster*. *J. Neurophysiol.* 102, 875–885

- Whitaker, K.W. et al. (2011) Serotonergic modulation of startle-escape plasticity in an African cichlid fish: a single-cell molecular and physiological analysis of a vital neural circuit. *J. Neurophysiol.* 106, 127–137
- Berón De Astrada, M. et al. (2013) Behaviorally related neural plasticity in the arthropod optic lobes. *Curr. Biol.* 23, 1389–1398
- Roberts, A.C. et al. (2016) Long-term habituation of the C-start escape response in zebrafish larvae. *Neurobiol. Learn. Mem.* 134, 360–368
- Magani, F. et al. (2016) Predation risk modifies behaviour by shaping the response of identified brain neurons. *J. Exp. Biol.* 219, 1172–1177
- Sitaraman, D. et al. (2017) Discrete Serotonin Systems Mediate Memory Enhancement and Escape Latencies after Unpredicted Aversive Experience in *Drosophila* Place Memory. *Front. Syst. Neurosci.* 11, 1–11
- Tomsic, D. et al. (2017) The predator and prey behaviors of crabs: from ecology to neural adaptations. *J. Exp. Biol.* 220, 2318–2327 \*
- Almada, R.C. et al. (2018) Stimulation of the Nigroreticular Pathway at the Level of the Superior Colliculus Reduces Threat Recognition and Causes a Shift From Avoidance to Approach Behavior. *Front. Neural Circuits* 12, 1–9
- Burgos, A. et al. (2018) Nociceptive interneurons control modular motor pathways to promote escape behavior in *Drosophila*. *Elife* 7, 1–28

### ***Cortical and neuromodulatory input to the superior colliculus***

- Fries, W. (1984) Cortical projections to the superior colliculus in the macaque monkey: A retrograde study using horseradish peroxidase. *J. Comp. Neurol.* 230, 55–76
- Ueda, S. et al. (1985) The organization of serotonin fibers in the mammalian superior colliculus. An immunohistochemical study. *Anat Embryol* 173, 13–21
- Beitz, A.J. et al. (1986) Differential Origin of Brainstem Serotonergic Projections to the Midbrain Periaqueductal Gray and Superior Colliculus of the Rat. *J. Comp. Neurol.* 250, 498–509
- May, P.J. (2006) The mammalian superior colliculus: Laminar structure and connections. *Prog. Brain Res.* 151, 321–378
- Muthuraju, S. et al. (2016) Dopamine D2 receptors regulate unconditioned fear in deep layers of the superior colliculus and dorsal periaqueductal gray. *Behav. Brain Res.* 297, 116–123
- Savage, M.A. et al. (2017) Segregated fronto-cortical and midbrain connections in the mouse and their relation to approach and avoidance orienting behaviors. *J. Comp. Neurol.* 525, 1980–1999

### ***Associative learning expands the ability to detect threats***

- LeDoux, J.E. et al. (1988) Different projections of the central amygdaloid nucleus mediate autonomic and behavioral correlates of conditioned fear. *J. Neurosci.* 8, 2517–2529
- Griffin, A.S. et al. (2001) Learning specificity in acquired predator recognition. *Anim. Behav.* 62, 577–589
- LeDoux, J. (2003) The emotional brain, fear, and the amygdala. *Cell. Mol. Neurobiol.* 23, 727–38 \*
- Gross, C.T. and Canteras, N.S. (2012) The many paths to fear. *Nat. Rev. Neurosci.* 13, 651–658 \*
- Pellman, B.A. and Kim, J.J. (2016) What Can Ethobehavioral Studies Tell Us about the Brain's Fear System? *Trends Neurosci.* 39, 420–431 \*
- Mitchell, M.D. et al. (2015) Learning to distinguish between predators and non-predators: Understanding the critical role of diet cues and predator odours in generalisation. *Sci. Rep.* 5, 1–10
- Tovote, P. et al. (2015) Neuronal circuits for fear and anxiety. *Nat. Rev. Neurosci.* 16, 317–331 \*

### ***Vigilance and active risk assessment enhance threat detection***

- Elgar, M. (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* 64, 13–33 \*
- Stankowich, T. and Blumstein, D.T. (2005) Fear in animals: A meta-analysis and review of risk assessment. *Proc. R. Soc. B Biol. Sci.* 272, 2627–2634 \*
- Hemmi, J.M. and Pfeil, A. (2010) A multi-stage anti-predator response increases information on predation risk. *J. Exp. Biol.* 213, 1484–1489
- Somerville, L.H. et al. (2011) Human bed nucleus of the stria terminalis indexed hypervigilant threat monitoring. *Biol. Psychiatry* 68, 416–424
- Pays, O. et al. (2013) Foraging in groups allows collective predator detection in a mammal species without alarm calls. *Behav. Ecol.* 24, 1229–1236
- Lee, S. et al. (2013) Direct Look from a Predator Shortens the Risk-Assessment Time by Prey. *PLoS One* 8, e64977
- Chivers, D.P. et al. (2016) Risk assessment and predator learning in a changing world: Understanding the impacts of coral reef degradation. *Sci. Rep.* 6, 1–7
- McNaughton, N. and Corr, P.J. (2018) Survival circuits and risk assessment. *Curr. Opin. Behav. Sci.* 24, 14–20
- Lojowska, M. et al. (2018) Visuocortical changes during a freezing-like state in humans. *Neuroimage* 179, 313–325
- Blank, D.A. (2018) Escaping behavior in goitered gazelle. *Behav. Processes* 147, 38–47

## **Decision processes and economics control the onset of escape**

- Cooper, W.E. and Frederick, W.G. (2007) Optimal flight initiation distance. *J. Theor. Biol.* 244, 59–67
- Samia, D.S.M. et al. (2016) Fifty years of chasing lizards: New insights advance optimal escape theory. *Biol. Rev.* 91, 349–366 \*
- Blumstein, D.T. et al. (2016) Escape behavior: dynamic decisions and a growing consensus. *Curr. Opin. Behav. Sci.* 12, 24–29 \*
- Cooper, W.E. (2016) Fleeing to refuge: Escape decisions in the race for life. *J. Theor. Biol.* 406, 129–136 \*
- Tätté, K. et al. (2018) Towards an integrated view of escape decisions in birds: relation between flight initiation distance and distance fled. *Anim. Behav.* 136, 75–86

## **Behavioural state and social context control defensive behaviours**

- Bellman, K.L. and Krasne, F.B. (1983) Adaptive complexity of interactions between feeding and escape in crayfish. *Science.* 221, 779–781
- Cooper, W.E. (1997) Factors Affecting Risk and Cost of Escape by the Broad-Headed Skink (*Eumeces laticeps*): Predator Speed, Directness of Approach, and Female Presence. *Herpetologica* 53, 464–474
- Díaz-Uriarte, R. (1999) Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. *Proc. R. Soc. B Biol. Sci.* 266, 2457–2464
- Lin, D. et al. (2011) Functional identification of an aggression locus in the mouse hypothalamus. *Nature* 470, 221–6
- Issa, F.A. et al. (2012) Neural Circuit Reconfiguration by Social Status. *J. Neurosci.* 32, 5638–5645
- Madden, J.R. and Whiteside, M.A. (2014) Selection on behavioural traits during ‘unselective’ harvesting means that shy pheasants better survive a hunting season. *Anim. Behav.* 87, 129–135
- Clinchy, M. et al. (2013) Predator-induced stress and the ecology of fear. *Funct. Ecol.* 27, 56–65
- Niemelä, P.T. et al. (2015) Personality-related survival and sampling bias in wild cricket nymphs. *Behav. Ecol.* 26, 936–946
- Falkner, A.L. et al. (2016) Hypothalamic control of male aggression-seeking behavior. *Nat. Neurosci.* 19, 596–604
- Blake, C.A. and Gabor, C.R. (2016) Exploratory behaviour and novel predator recognition: behavioural correlations across contexts. *J. Fish Biol.* 89, 1178–1189
- Livneh, Y. et al. (2017) Homeostatic circuits selectively gate food cue responses in insular cortex. *Nature* 546, 611
- Park, C. et al. (2018) Effects of Social Experience on the Habituation Rate of Zebrafish Startle Escape Response: Empirical and Computational Analyses. *Front. Neural Circuits* 12, 1–16

## **Freezing as a defence mechanism**

- O'Brien, T.J. and Dunlap, W.P. (1975) Tonic immobility in the blue crab (*Callinectes sapidus*, Rathbun): Its relation to threat of predation. *J. Comp. Physiol. Psychol.* 89, 86–94
- Bonenfant, M. and Kramer, D.L. (1996) The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behav. Ecol.* 7, 299–303
- Mongeau, R. et al. (2003) Neural correlates of competing fear behaviors evoked by an innately aversive stimulus. *J. Neurosci.* 23, 3855–3868
- Edut, S. and Eilam, D. (2004) Protean behavior under barn-owl attack: Voles alternate between freezing and fleeing and spiny mice flee in alternating patterns. *Behav. Brain Res.* 155, 207–216
- Eilam, D. (2005) Die hard: A blend of freezing and fleeing as a dynamic defense - implications for the control of defensive behavior. *Neurosci. Biobehav. Rev.* 29, 1181–1191 \*
- Roelofs, K. (2017) Freeze for action: Neurobiological mechanisms in animal and human freezing. *Philos. Trans. R. Soc. B Biol. Sci.* 372, 20160206 \*

## **Escape tactics**

### **Optimising the speed of escape**

- Walker, J.A. et al. (2005) Do faster starts increase the probability of evading predators? *Funct. Ecol.* 19, 808–815
- Seamone, S. et al. (2014) Sharks modulate their escape behavior in response to predator size, speed and approach orientation. *Zoology* 117, 377–382
- Wheatley, R. et al. (2015) How Fast Should an Animal Run When Escaping? An Optimality Model Based on the Trade-Off between Speed and Accuracy. *Integr. Comp. Biol.* 55, 1166–1175
- Nasir, A.F.A.A. et al. (2017) Optimal running speeds when there is a trade-off between speed and the probability of mistakes. *Funct. Ecol.* 31, 1941–1949
- Nair, A. et al. (2017) A faster escape does not enhance survival in zebrafish larvae. *Proc. R. Soc. B Biol. Sci.* 284, 20170359

### *Escape trajectories and tactics*

- Arnott, S. et al. (1999) Escape trajectories of the brown shrimp crangon crangon, and a theoretical consideration of initial escape angles from predators. *J. Exp. Biol.* 202 (Pt 2), 193–209
- Lindeyer, C.M. and Reader, S.M. (2010) Social learning of escape routes in zebrafish and the stability of behavioural traditions. *Anim. Behav.* 79, 827–834
- Mäkeläinen, S. et al. (2014) Different escape tactics of two vole species affect the success of the hunting predator, the least weasel. *Behav. Ecol. Sociobiol.* 68, 31–40
- Cooper, W.E. and Sherbrooke, W.C. (2016) Strategic Escape Direction: Orientation, Turning, and Escape Trajectories of Zebra-Tailed Lizards (*Callisaurus draconoides*). *Ethology* 122, 542–551
- Herbert-Read, J.E. et al. (2017) Escape path complexity and its context dependency in Pacific blue-eyes (*Pseudomugil signifer*). *J. Exp. Biol.* 220, 2076–2081
- Fukutomi, M. and Ogawa, H. (2017) Crickets alter wind-elicited escape strategies depending on acoustic context. *Sci. Rep.* 7, 1–8

### **Neuroethology of escape and decision-making: reviews**

- Adams, G.K. et al. (2012) Neuroethology of decision-making. *Curr. Opin. Neurobiol.* 22, 982–989
- Blumstein, D.T. et al. (2016) Escape behavior: dynamic decisions and a growing consensus. *Curr. Opin. Behav. Sci.* 12, 24–29
- Korn, H. and Faber, D.S. (2005) The Mauthner cell half a century later: A neurobiological model for decision-making? *Neuron* 47, 13–28
- Lagos, P.A. (2017) A review of escape behaviour in orthopterans. *J. Zool.* 303, 165–177
- Ledoux, J. and Daw, N.D. (2018) Surviving threats: Neural circuit and computational implications of a new taxonomy of defensive behaviour. *Nat. Rev. Neurosci.* 19, 269–282
- McNaughton, N. and Corr, P.J. (2018) Survival circuits and risk assessment. *Curr. Opin. Behav. Sci.* 24, 14–20
- Mobbs, D. (2018) The ethological deconstruction of fear(s). *Curr. Opin. Behav. Sci.* 24, 32–37