

1 Who would have thought that 'Jaws' also has brains? Cognitive
2 functions in elasmobranchs

3
4
5
6
7 Published in Animal Cognition (2015)18:19-37

8
9 Uncorrected Final Submission –

10 For a corrected version, please refer to the Journals Web Site
11 <http://link.springer.com/article/10.1007/s10071-014-0762-z>
12

13
14 Schluessel V.

15
16
17 Institute of Zoology
18 Rheinische-Friedrich-Wilhelm Universität Bonn,
19 Poppelsdorfer Schloss
20 Meckenheimer Allee 169
21 53115 Bonn
22 Germany

23
24 Tel: +49 228 735476

25 Fax: +49 228 5458

26 Email: v.schluessel@uni-bonn.de
27

28 **Abstract**

29 Adaptation of brain structures, function and higher cognitive abilities most likely have
30 contributed significantly to the evolutionary success of elasmobranchs, but these traits
31 remain poorly studied when compared to other vertebrates, specifically mammals.
32 While the pallium of non-mammalian vertebrates lacks the mammalian neocortical
33 organization responsible for all cognitive abilities of mammals, several behavioural and
34 neuroanatomical studies in recent years have clearly demonstrated that
35 elasmobranchs, just like teleosts and other non-mammalian vertebrates, can
36 nonetheless solve a multitude of cognitive tasks. Sharks and rays can learn and
37 habituate, possess spatial memory and can orient according to different orientation
38 strategies, remember spatial and discrimination tasks for extended periods of time, use
39 tools, can imitate and learn from others, distinguish between conspecifics and
40 heterospecifics, discriminate between either visual objects or electrical fields, can
41 categorize visual objects and perceive illusory contours as well as bilateral symmetry.
42 At least some neural correlates seem to be located in the telencephalon, with some
43 pallial regions matching potentially homologous areas in other vertebrates where
44 similar functions are being processed. Results of these studies indicate that the
45 assessed cognitive abilities in elasmobranchs are as well developed as in teleosts or
46 other vertebrates, aiding them in fundamental activities such as food retrieval, predator
47 avoidance, mate choice and habitat selection.

48

49

50 Introduction

51 *Cognition*

52 In order to cope with changing environments and match new requirements animals
53 need to adjust their behaviour accordingly. One way to do this is by learning. In its
54 basic form learning is defined as 'a skill, knowledge or behaviour gained through study
55 or experience' and is therefore advantageous to just about any form of life. As
56 expected, different types and degrees of learning have been observed in just about
57 any vertebrate and invertebrate taxa studied, even in simple organisms such as the
58 amoebalike cell *Physarum polycephalum* (Saigusa et al. 2008).

59

60 Learning and memory are recognized as cognitive functions; but terms like 'cognition'
61 or 'cognitive ability' are often used ambiguously and have to be defined for each
62 context they are used in. Here, both are general terms that refer to all processes of
63 perceiving, recognizing, conceiving, judging, reasoning, imagining and all associated
64 learning abilities. Higher cognitive abilities specifically refer to more advanced
65 processes such as the construction of cognitive spatial maps, declarative memory
66 retention, categorization and self-recognition as well as a range of social learning
67 functions (e.g. imitative learning through the observation of others). Higher cognitive
68 functions do not include simple innate behaviours, such as the jamming avoidance
69 response in weakly electric fish (Heiligenberg 1986), electrosensory guided prey
70 capture in paddlefish (Wilkens and Hofmann 2002) or the ability of some fish to sort
71 food particles from stones while chewing (Finger 2008). Cognitive abilities are
72 obviously crucial for behaviours involved in localizing and identifying predators or prey,
73 hiding places, sexual partners or other individuals and moving within complex spatial
74 habitats.

75

76 Adaptation of brain structures, function and higher cognitive abilities most likely have
77 contributed significantly to the evolutionary success of both teleosts and
78 elasmobranchs (sharks, skates and rays), but these traits remain poorly studied in both
79 groups, and specifically in the latter, when compared to mammals. A quick search on
80 the Web of Knowledge (<http://apps.webofknowledge.com>, 17.5.2013) yielded 159.552
81 hits for 'cognition and mammals' ('primates': 138,197), compared to 1.742 for 'cognition
82 and fish', which equates roughly to about 29 cognition studies for each species of

83 mammal, compared to about 0.06 studies for each species of fish. While both the web-
84 search and the calculation are obviously crude approximations, these numbers
85 nonetheless clearly indicate the overwhelming prevalence of studies dealing with
86 cognitive functions of mammals or primates in particular.

87 One of the most striking differences in brain morphology between different groups of
88 vertebrates is the lack of the typical mammalian neocortex organization in fish,
89 amphibians and sauropsids, despite the fact that the vertebrate brain follows a general
90 'Bauplan' (Wullimann 1997; Northcutt 2011). It is well known that most, if not all, higher
91 cognitive abilities of mammals are dependent on cortical circuits and a mammal whose
92 cortex has been ablated, can no longer perform higher cognitive tasks (Kaas 1987).
93 Indeed, removal of the telencephalon in mammals abolishes most behavior (Grill and
94 Norgren, 1978). For a long time, the absence of a cortex in non-mammalian species,
95 and in case of fish their phylogenetic age, led to the common misconception that fish
96 but also amphibians and reptiles are more instinct-driven or 'primitive' than mammals
97 and lack cognitive abilities altogether. This however, as we now know, is not true.
98 Surprisingly though, removal of the telencephalon in teleosts causes neither a
99 noticeable disruption to the fish's swimming or feeding behavior nor impairs any
100 sensory functions apart from olfaction (e.g. Hofmann 2001), indicating that not all
101 cognitive functions are exclusively situated in the telencephalon. Not only fish, but also
102 other non-mammalian species have shown to perform many cognitive tasks despite
103 the absence of a six-layered neocortex; birds for example have astonishing cognitive
104 abilities (e.g. Salwiczek et al. 2012; Shettleworth, 2010), but lack a laminated forebrain
105 and, according to some scientists, only have a relatively small dorsal pallium or
106 neocortex homologue (Striedter 1997; Puelles et al. 2000; but see Butler et al. 2011;
107 Karten 2013). Even invertebrates (e.g. bees, wasps, cephalopods, crustaceans) that
108 have substantially smaller and very differently organized brains than vertebrates, show
109 very sophisticated cognitive abilities (e.g. Srinivasan 2010; Chittka and Skorupski
110 2011; Menzel 2012; Giurfa 2013). So, in the absence of a mammalian cortex, cognitive
111 abilities - which are undoubtedly present - must be localized and based in some other
112 neural substrates.

113 However, while there has been an upsurge in behavioural studies on cognition in
114 teleosts in the last 25 years and more recently in elasmobranchs, only a few studies
115 have tried to uncover the neuronal substrates or neuronal circuits that allow fish to

116 perform higher cognitive tasks. This is unfortunate, as pallial development and
117 complexity in fish varies tremendously, not just between Chondrichthyans and
118 Osteichthyes but also between different species within these groups. Most strikingly,
119 as opposed to an eversion process found in Actinopterygians, the elasmobranch
120 telencephalon undergoes the craniate-characteristic evagination process during
121 morphogenesis, which places brain areas in positions not always easily compared to
122 those of other fish, such as teleosts (Smeets et al., 1983). Nonetheless, previous
123 studies have clearly demonstrated that teleosts, and - as will be seen later - also
124 elasmobranchs, are in some respect behaviourally and neuronally as complex as
125 mammals and can solve a multitude of cognitive tasks (for a review see Brown et al.
126 2011). Indeed, for a few non-mammalian species, forebrain areas have already been
127 found to be homologous to mammalian forebrain areas, despite (substantial)
128 differences in their connectivity and histology (Reiner et al. 2004). These differences
129 include the lack of the mammalian six-layered neocortex (including the three layered
130 hippocampus or so-called archicortex in mammals), different ascending projections
131 from the midbrain and diencephalon to the telencephalon, differences in pallial terminal
132 fields of sensory projections, as well as specializations in diencephalic organization,
133 i.e. in fish a rather complex and differentiated hypothalamus. These results were
134 obtained by neuroanatomical and neuromolecular mapping as well as theoretical
135 approaches in fish (Mueller et al. 2008; Mueller and Wullimann 2009; Rodriguez-
136 Moldes 2009), birds (e.g. Herold et al. 2012; Puelles et al. 2013), amphibians (Moreno
137 and Gonzalez 2007; Roth et al. 2004) and reptiles (Font et al. 1995; Martínez-García
138 et al. 2009). There is also some evidence that both a hippocampal and amygdala
139 functional equivalence - despite their different histological organization - appear to
140 represent true hippocampus and pallial amygdala homologues in fish (Wullimann and
141 Mueller 2004; Rodriguez et al. 2006; Portavella et al. 2005; Costa et al. 2011) and
142 exists also at least in birds and amphibians (e.g. Dicke and Roth 2007; Atoji and Wild
143 2006; Abellan et al. 2013).

144

145 *Cognition in sharks*

146 Sharks, rays and chimaeras comprise the class Chondrichthyes (cartilaginous fishes),
147 which are the oldest extant jawed vertebrates. The class is divided into two sister taxa,
148 the Elasmobranchii (sharks, skates and rays) and the Holocephali (chimaeras and
149 elephantfishes) (Compagno, 1999). Today, there are about 1200 species (Compagno,

150 1999), which inhabit almost every aquatic environment and hold a key phylogenetic
151 position to understanding brain evolution in jawed vertebrates. Both sharks and rays
152 show sophisticated behaviors, have a complex biology and are equipped with sensory
153 systems that are perfectly adapted to life underwater (Hueter et al. 2004). However,
154 despite elaborate research on many aspects of elasmobranch biology, the information
155 on the scope of elasmobranch learning and memory as well as knowledge about the
156 corresponding brain areas is still limited. Guttridge et al. (2009) published a review
157 covering the last 50 years of research on the topic and found just over 30 studies
158 related to some form of learning. In many of those studies, however, learning was only
159 assessed as a byproduct in the context of studying something else, like a sensory
160 system. These early investigations provided a first indication that sharks and rays can
161 learn and possibly even solve cognitive tasks (e.g. Clarke 1959; Clark 1963; Malyukova
162 et al. 1963; Wright and Jackson 1964; Aronson 1967; Banner 1967; Nelson 1967;
163 Gruber and Schneiderman 1975; Gruber and Cohen 1978; Rasmussen and Schmidt
164 1992) but rigorous testing in the form of controlled laboratory experiments was in most
165 cases lacking. Shark research in the 1940s and 50s was mainly driven by the desire
166 to find suitable shark deterrents and the few behavioral experiments conducted during
167 this time and thereafter were often only performed on one or two individuals, in many
168 cases under problematic experimental conditions (e.g. animals were not tested
169 individually) and often without adequate controls. Few studies followed throughout the
170 80s and 90s (e.g. McManus 1984), possibly due to the difficulty of obtaining and
171 maintaining sharks in a laboratory or creating controllable experimental conditions in
172 the field. The general public opinion was also very shark-hostile due to blockbusters
173 like 'Jaws' in the 70s manifesting the image of the shark as a mindless killing machine.
174 In subsequent years, this may have also negatively affected research interest within
175 this area or available research funding. In more recent years though, public perception
176 of sharks has changed considerably, with many people, scientists and non-scientists
177 alike, now being highly aware of the precarious situation many shark species are in
178 due to their high susceptibility to overfishing, their general exploitation, and the impacts
179 of environmental degradation and pollution. Along with losing the brand mark of being
180 a primitive monster, experiments on cognitive and specifically higher cognitive
181 functions in sharks and rays, both on a behavioral as well as a neuroanatomical level,
182 have increased substantially. For example, Schluessel and Bleckmann (2005; 2012)
183 provided evidence for a spatial memory system and different orientation mechanisms

184 in freshwater stingrays (*Potamotrygon motoro*) and bamboo sharks (*Chiloscyllium*
185 *punctatum* and *C. griseum*), Guttridge et al. (2013) observed social learning in lemon
186 sharks (*Negaprion brevirostris*), and Kuba et al. (2009) found tool use in freshwater
187 stingrays (*Potamotrygon falkneri*).

188

189 Like any other trait, cognitive abilities and their neuromorphological correlates are
190 subject to selection during evolution (Thornton et al. 2012). Elasmobranchs are often
191 apex predators and have had roughly 450 Million years to evolve; it would have been
192 highly surprising if cognitive abilities had been evolutionarily stagnant in these animals
193 and in fact, as will be shown, they were not. Also, many important ecological factors,
194 such as foraging, tool use and social learning, can drive evolutionary neuroanatomical
195 changes (e.g. Pollen et al. 2007; Shumway 2008; Kotrschal and Taborsky 2010;
196 Ebbesson and Braithwaite 2012; Lefebvre 2013). For example, higher cognitive
197 abilities are required to find food in complex habitats compared to more simple or
198 unstructured habitats. As a result, associated brain regions, e.g. the hippocampus (or
199 its homologues), are enlarged in species that live and forage in complex environments
200 (e.g. Sherry et al. 1989, 1992; Lucas et al. 2004). Similarly, it has been suggested that
201 brain size in sharks may correlate with habitat, lifestyle or cognitive capabilities
202 (Bauchot et al. 1976; Northcutt, 1977; Yopak et al. 2007; Yopak and Frank 2009; Yopak
203 2012). Larger brains may be found in pelagic or benthopelagic sharks that live in
204 complex (reef-) habitats and pursue more active predation strategies (reviewed in
205 Yopak 2012). Larger brains have also been found in more social species, those that
206 aggregate and exhibit complex courtship or mating behaviours (reviewed in Yopak
207 2012). As mentioned previously, in teleosts, other vertebrates and also in
208 elasmobranchs the telencephalon and specifically the pallium is one of the most likely
209 neural substrates to be involved in the processing of cognitive information. Several
210 reviews on the brain and more recently specifically on the neuroecology of
211 elasmobranchs have been provided by Ebbesson (1972, 1980), Northcutt (1977,
212 1978), Collin (2012) and Yopak (2012).

213

214 The following review gathers together what has been learned so far about the (higher)
215 cognitive abilities of elasmobranchs, i.e. data, which has mainly been collected over
216 the past five years. As simple learning abilities of sharks have previously been
217 reviewed thoroughly by Guttridge et al. (2009), learning strategies as such will not be

218 mentioned (as for example in the case of using classical and operant conditioning
219 schemes to determine sensory thresholds). Eight research areas will be described,
220 whenever possible both on a behavioural and a neuroanatomical level. These areas
221 are spatial memory and orientation, problem solving and tool use, social cognition,
222 avoidance learning, object recognition and categorization, symmetry perception,
223 recognition of illusory contours and memory retention. Results will briefly be
224 compared to the more extensive data collected on teleosts (most of which has been
225 reviewed in Brown et al. 2011).

226

227 1. Spatial memory and orientation

228 Migration, navigation and orientation, both on a small and large scale, involve some
229 form of spatial sense. Multiple studies have shown that sharks engage in such activities
230 and that various mechanisms can be employed in the process (reviewed in Guttridge
231 et al. 2009). Specifically, long distance migration often seems to be a product of
232 following sensory gradients or selected sensory cues, as for example in the case of
233 salmon using olfactory cues for homing (Dittman and Quinn 1996) or in the case of
234 hammerhead sharks (*Sphyrna lewini*) which may be using the earth's magnetic field
235 for navigating (Klimley 1993; Meyer, 2005). Therefore, not all spatial mechanisms or
236 strategies can be considered as examples of (higher) cognitive learning. However,
237 animals may not only follow sensory gradients or use single sensory cues to locate a
238 goal but may learn and remember the relationship between different environmental
239 cues and then store this information as a mental map in some neural substrate using
240 spatial memory (O'Keefe and Nadel, 1978). This is referred to as using a 'cognitive
241 spatial map' or an 'allocentric' strategy (also termed 'place procedure' in Fuss et al.
242 2014) and is basically something like an 'internal street map' the animal is using.
243 Obviously, this provides a certain degree of flexibility with regard to the presence or
244 absence of single environmental features and enables animals to proceed to the goal
245 via short cuts or novel routes even when released from unfamiliar sites. Although, it
246 will always be referred to a 'visual' cognitive map from here on, cognitive maps can
247 also be based on other sensory systems (e.g. the lateral line system in blind cave fish,
248 Teyke 1989). In contrast to employing such a cognitive mapping system, an animal
249 can also use alternative strategies, including one of two 'taxon' or 'egocentric
250 strategies' as defined by O'Keefe and Nadel (1978). In these strategies, the animal
251 uses either simple visual cues (beacon or guidance learning) to approach or avoid

252 locations or uses a body centered reference system in order to orient (cue or turn
253 procedure), hence it can only reach the goal by proceeding from one familiar object to
254 the next, or by approaching the goal by performing a body-centered turn in response
255 to a particular cue. In these cases, performance is quite easily disrupted by habitat
256 alteration or object deletion (O'Keefe and Nadel, 1978). Further strategies include dead
257 reckoning, compass orientation and local views; however, only a (cognitive) spatial
258 mapping strategy provides an example of a higher cognitive task.

259

260 Early investigations on spatial memory and orientation mechanisms in elasmobranchs
261 were performed by O'Gower (1995) and Edren and Gruber (2005) who tested homing
262 abilities of displaced Port Jackson (*Heterodontus portusjacksoni*) and lemon sharks
263 (*Negaprion brevirostris*) in the wild. Results indicated some form of spatial memory in
264 both species and considering that both returned to the very specific sites they had been
265 removed from it may have been possible that, at least in the final stages of homing,
266 complex cognitive mechanisms, e.g. a cognitive spatial map, were used for orientation.
267 Unfortunately though, the orientation mechanisms employed were not investigated in
268 these studies, and another study by Sundström et al. (2001) showed that blinded,
269 displaced lemon sharks could also return to their original capture sites. This may
270 indicate that not only vision (including a cognitive spatial map) but also other sensory
271 mechanisms may have played a role in these experiments. Meyer et al. (2010)
272 analysed movement patterns of tiger sharks (*Galeocerdo cuvier*) and Galapagos
273 sharks (*Carcharhinus galapagensis*) in detail, concluding that tiger sharks may use
274 cognitive spatial maps for orientation while moving between different foraging areas.
275 Also, both tiger and thresher sharks (*Alopias vulpinus*) perform 'directed walks'
276 (moving towards a known goal, Nams 2006), indicative of a more intricate knowledge
277 of the surrounding area (Papastamatiou et al. 2011). Conclusive support for some sort
278 of place learning, possibly even the construction of a cognitive spatial map came from
279 laboratory experiments on freshwater stingrays (*Potamotrygon motoro*) (Schluessel
280 and Bleckmann 2005). Twelve individuals were trained for 18 months in a four arm-
281 maze where they learned to retrieve food from a specialized feeding apparatus and
282 solved spatial tasks using either visual cues or body centred turns. Rays trained in a
283 place procedure (allocentric group) successfully utilized a broad variety of extramaze
284 visual cues to reach the goal via novel routes starting from unfamiliar locations, while
285 rays trained in a task for which either a place or a cue procedure (ego-allocentric group)

286 could have been used primarily solved the task on the basis of the latter. In 2012,
287 similar experiments were performed on sharks (*Chiloscyllium sp.*) using either intra- or
288 extramaze visual cues, and results matched those previously obtained for stingrays
289 (Schluessel and Bleckmann 2012; Fuss et al. 2014 a, b). In the presence of visual
290 landmarks, sharks were either trained in a turn procedure without a fixed goal location
291 (egocentric) or in a turn procedure with a fixed goal location (ego-allocentric) (Fuss et
292 al. 2014b). Sharks in both groups successfully mastered the task predominantly but
293 not exclusively on the basis of turn responses, as indicated by transfer tests (T1;
294 Fig.1a, b); in the absence of visual extra-maze cues, turn responses were used
295 exclusively (elimination; Figure 1a). Ego-allocentrically trained sharks, just like
296 stingrays and goldfish (Rodriguez et al. 1994), also chose arms corresponding to the
297 correct turn response and to a place response significantly more often than the third
298 arm corresponding to neither of the two (Fig. 1b). Sharks trained in complex place
299 learning or allocentric orientation in a second set up (Fuss et al. 2014a; Fig. 2) used
300 intra-maze cues instead of directional information to locate the goal, and like the
301 stingrays navigated independently of single landmarks. In the absence of all visual
302 landmarks orientation was lost. Surprisingly, a rearrangement of the spatial structure
303 of the set up interfered with orientation capabilities of five out of seven individuals in
304 one task (T6) and six out of seven in another (T7) due to unknown reasons (Figure 2).
305 Again, similar results have been obtained for goldfish (Vargas et al. 2004).

306
307 Behavioral studies in sharks were followed up by selective lesion experiments, which
308 showed that the dorso-medial pallium in the telencephalon plays a crucial role in
309 processing more complex place learning information (Fuss et al. 2014a) but is not
310 implicated in the processing of egocentric information, i.e. turn procedures (Fuss et al.
311 2014b). Accordingly, as in other vertebrates, different neural substrates seem to be
312 responsible for different spatial functions and mechanisms in sharks. Ablation of the
313 medial pallium in sharks also caused similar impairments in spatial learning and
314 memory as lateral pallial ablations produced in goldfish. This indicates that the dorso-
315 medial portion of the pallium may be comparable to the hippocampus of land
316 vertebrates and the lateral pallium (area dorsalis pars lateralis) of teleosts (Fuss et al.
317 2014a, b).

318

319 An extensive literature exists on spatial cognition and orientation in teleosts (for
320 reviews see Odling-Smee et al. 2006 and Rodriguez et al. 2006), providing
321 comprehensive information on the different spatial strategies, cues and mechanisms
322 used by fish to orient and navigate. The telencephalon (specifically the lateral pallium)
323 plays a crucial role in complex place learning and spatial memory in goldfish (e.g. Salas
324 et al. 1996a, b; Lopez et al. 2000; Duran et al. 2008, 2010; Costa et al. 2011) but
325 depending on the spatial strategy used, also non-telencephalic structures (e.g. the
326 cerebellum) may be involved (e.g. Lopez et al. 2000). In some species, sex specific
327 differences in regards to spatial demands exist both behaviorally and neuronally (Costa
328 et al. 2011). Most research on spatial cognition in fishes consists of purely behavioral
329 studies (e.g. Aronson 1951; Kleerekoper et al. 1970, 1974; Roitblatt et al. 1982; Reese
330 1989; Warburton 1990; Lopez et al. 1999, 2000; Hughes and Blight 2000; Sovrano et
331 al. 2002, 2007; Burt de Perrera and Macias Garcia 2003; Odling-Smee and Braithwaite
332 2003; Odling-Smee et al. 2008; Fukumori et al. 2009; Burt de Perrera and Holbrook
333 2011, 2012; Vargas et al 2011), and comparatively few purely neuroanatomical or
334 molecular studies exist (reviewed in Brown et al. 2011; Demski 2013; Wood et al.
335 2012). In one exceptional series of studies on the goldfish, both approaches were used
336 complementarily (reviewed in Rodriguez et al. 2006).

337

338 2. Problem solving and tool use

339 Tool use in teleosts was recently reviewed by Brown (2012) who adapted the definition
340 of tool use by Jane Goodall, 'the active manipulation of an external object in the
341 attainment of a goal' as the most suitable for fish. Fish need to manipulate objects, for
342 instance to increase feeding efficiency and obtain access to food items, move objects
343 or to clean nests; but there are not many examples for tool use in fish in general
344 (Bshary et al. 2002; Brown 2012), and only one for the elasmobranchs in particular.
345 Kuba et al. (2010) investigated the ability of five sub-adult freshwater stingrays
346 (*Potamotrygon castexi*) to use water as a tool to extract food from a tube. All rays
347 quickly accomplished the task but interestingly applied different methods in the
348 process, such as undulating fin movements, suction and/or a combination of both. In a
349 second experiment, the formerly open tube was now closed at one end, which was
350 signaled by a different marker (black) than the open end (white). Rays needed more
351 sessions than in the first task to perform successfully and again different strategies
352 were applied by the five individuals, both for locating the open tube end and for the

353 extraction of food from the tube. Only one male used the visual markers provided for
354 guidance; the other rays applied trial and error learning, whereby animals sometimes
355 had to inspect both ends one after another (correction of an incorrect choice). In
356 regards to the extraction strategies used, only one male successfully produced water
357 jets blown into the pipe to retrieve the food; all other individuals shifted their preferred
358 strategies towards using both undulating movements and suction together instead of
359 using either strategy alone. Water use to simply uncover hidden prey (e.g. by blowing
360 or fin movements) has also been reported for other sharks and ray species (reviewed
361 in Hueter et al. 2004), but is not really considered a cognitive task here. The most
362 famous example of tool use in teleosts is probably provided by archer fish (*Toxotes*
363 *jaculatrix*) which expel jets of water to shoot down insects from above the water surface
364 despite the air/water interphase. Archer fish can determine the flight path, the exact
365 point of impact of the prey when falling into the water, the absolute size of their prey
366 and can even hit moving targets (Schuster et al. 2004, 2006). Some gouramis and
367 wrasses can also manipulate water jets for various purposes (reviewed in Brown 2012),
368 use anvils to open bivalves or scallops (Coyer, 1995; Jones et al. 2011), crush sea
369 urchins, remove spines or break large pieces into conveniently sized ones (Fricke,
370 1971; Wirtz 1996; Paško 2010). In case of several other activities, e.g. various cleaning
371 procedures, it is quite hard to determine if in fact any cognitive processing is required
372 or not. It seems rather likely that several of these behaviors may be stereotyped instead
373 of cognitive (Brown, 2012).

374

375 3. Social cognition

376 To my knowledge, the ability to recognize oneself has not been shown for any fish
377 species so far, but there are several studies showing that fish can identify individuals
378 of the same or other species (using various sensory modalities). Also, the ability to
379 obtain information through the observation of or the interaction with other individuals
380 occurs in several freshwater fishes regarding a wide range of behaviors (reviewed in
381 Bshary, 2006; Griffith and Ward, 2006). So far, only a few studies have assessed social
382 cognition, and explicitly learning through the observation of others, within the
383 elasmobranchs (Guttridge et al. 2009; 2011; 2013; Thonhauser et al. 2013). Earlier
384 studies had already shown that sharks aggregate in groups or schools that may be
385 size- or sex-specific (e.g. Klimley and Nelson 1981; Economakis and Lobel 1998; Sims
386 2003; Heupel and Simpfendorfer 2005; Guttridge et al. 2009) and conform to certain

387 social hierarchies (e.g. Myrberg and Gruber 1974; Klimley and Nelson 1981; Jacoby
388 et al. 2010). However, these studies did not investigate cognitive aspects of such
389 behaviours. Instead of reflecting active and thereby 'cognitive' choices for some
390 unknown benefit, such aggregation behaviours could also just be 'passive
391 consequences' of irregular or localized resources or caused by something else that
392 cognitive functions are not involved in, or are not necessary for. Guttridge et al. (2009)
393 assessed social preferences in juvenile lemon sharks (*Negaprion brevirostris*) in more
394 detail and found that sharks of a certain age actively prefer to be social rather than
395 solitary. In two-choice experiments, sharks first actively had to choose between
396 spending time alone as opposed to being in pairs or in groups, and significantly
397 preferred the latter. When having to choose between size-matched conspecifics and
398 unmatched conspecifics, sharks of two to three years of age actively preferred the
399 former, while younger individuals showed no significant preference. In a last
400 experiment, where lemon and nurse sharks had to choose between spending time with
401 a conspecific or a heterospecific (*Ginglymostoma cirratum*), lemon sharks preferred
402 the conspecific. Active partner preferences and differing leadership roles were also
403 observed in a second study by Guttridge et al. (2011). Finally, Guttridge et al. (2013)
404 tested social learning abilities by training and comparing the performance of sharks in
405 a food-finding task. Naive individuals called 'observers' were paired either with 'sham'-
406 or 'real demonstrator' conspecifics (only real demonstrators were trained in a food
407 finding task) to observe if these naive sharks could acquire information through the
408 social interactions with the demonstrators. Results indicated that sharks that were
409 allowed to watch real demonstrators, i.e. sharks with previous experience in the task,
410 completed more task-related behaviours and were faster than sharks that were paired
411 with sham demonstrators (i.e. sharks that had no previous experience in the task).
412 Also, when tested in isolation, sharks that had previously been paired with
413 demonstrators again performed better and were faster than after having been paired
414 with sham-demonstrators. This shows that sharks imitated or learned from the
415 demonstrators, retained the acquired information for some period of time and applied
416 it when exposed to the experimental task while being alone. Social learning has also
417 been investigated in freshwater stingrays (*P. falkneri*) in a similar paradigm
418 (Thonhauser et al. 2013). Here, one group of stingrays was trained in a food retrieval
419 task (demonstrators), in which food had to be extracted from a tube while another
420 group (observers) was only trained after having watched the demonstrator rays from

421 the first group successfully perform this feat several times. The performance of the two
422 groups was compared and observers were found to need significantly fewer trials than
423 the demonstrators to successfully extract the food from the tube. Additionally, not only
424 did rays in the observer group learn faster, but they also applied the most successful
425 technique more often than less profitable ones, further indicating that they had copied
426 the behaviour of the experienced demonstrators.

427

428 Teleosts observe others to improve feeding efficiency (Coolen et al. 2003; Pike et al,
429 2010) and possibly imitate leader fish, taking their routes and reproducing their postural
430 change (Mazeroll and Montgomery 1995). Social learning furthermore occurs in the
431 process of improving anti-predator behavior (e.g. Suboski et al. 1990; Mathis et al.
432 1996), migrating behavior (e.g. Helfman and Schultz 1984; Laland and Williams 1997),
433 mate choice (e.g. Dugatkin 1992; Schlupp and Ryan 1997), food retrieval (Schuster et
434 al. 2004; Kendal et al. 2009) and aggressive behavior (e.g. Johnsson and Akerman
435 1999). Social or public information may be of different relevance to males and females
436 and is used accordingly (Webster and Laland 2011). Recognition of individuals, e.g.
437 shoalmates, occurs in several fish species (e.g. Griffith and Magurran 1997; Milinski et
438 al. 1990 a,b; Grosenick et al. 2007) and is either based on obvious phenotypic and
439 behavioural characteristics (such as size and colour), or on more subtle information, in
440 which case it is referred to as 'familiarity' (Griffith and Ward 2006). This phenomenon
441 may even extend to heterospecifics (Ward et al. 2003). Additionally, a range of fish
442 species recognizes kin (Griffith and Ward 2006), which may or may not be cognitively
443 driven as mechanisms can include vision, olfaction, acoustics and the major
444 histocompatibility complex (Myrberg and Riggio 1985; Griffith and Ward 2006;
445 Thünken et al. 2009). While a wide breadth of behavioural studies exists on the topic,
446 comparatively little to almost no research has been done to elucidate any of the neural
447 substrates underlying these behaviours. When fighting their mirror image, male
448 *Haplochromis burtoni* had a significantly higher expression of immediate early genes
449 in brain areas homologous to the mammalian amygdala than controls (Desjardins and
450 Fernald 2011).

451

452 4. Object recognition

453 Recognition and discrimination abilities are essential for a wide range of behaviours
454 including the selection of appropriate food sources, identification of prey and predators,

455 and the recognition of conspecifics, heterospecifics and potential partners as well as
456 of territories and home ranges. For any purpose, different sensory modalities can be
457 used, either alone or in combination. There are several experiments indicating simple
458 visual discrimination capabilities of geometric symbols for a range of elasmobranch
459 species. Graeber et al. (1972) and Graeber and Ebbesson (1973) successfully
460 demonstrated visual target discrimination of solid black and white panels as well as
461 striped panels in a few individuals of normal and tectum ablated nurse sharks
462 (*Ginglymostoma cirratum*). Tester and Kato (1966) and Aronson (1967) successfully
463 tested simple visual discrimination abilities (black vs. white targets) in several
464 Carcharhinid species and nurse sharks. Aronson (1967) compared shark learning
465 rates in a visual discrimination paradigm to those of mice and teleosts, and determined
466 that they learned about equally fast. Freshwater stingrays (*Potamotrygon motoro*) and
467 sharks (*Chiloscyllium punctatum* and *C. griseum*) relied on the visual system in various
468 place learning tasks (Schluessel and Bleckmann 2005; Schluessel and Bleckmann
469 2012; Fuss, et al. 2014 a, b). Stingrays also distinguished between a solid black and a
470 black and white striped target (Schluessel, unpublished data). Fuss et al. (2014c)
471 examined visual discrimination tasks in bamboo sharks, using two-dimensional (2D)
472 geometric stimuli. Sharks distinguished a square from two differently sized triangles, a
473 circle, a rhomboid and a cross. As training went on, the number of correct choices per
474 session increased significantly and in some cases, subsequent stimulus pairs were
475 distinguished faster than the two symbols in the original stimulus pair. Results indicated
476 that not only the positive stimulus but also the negative one was remembered and that
477 learning rates correspond to those found in teleosts. Following training, sharks were
478 tested in a reversal task (with the positive stimulus now being the negative one); as
479 expected more sessions were needed to achieve the learning criterion than in previous
480 training experiments but all sharks accomplished the task. The study clearly showed
481 that bamboo sharks can learn visual discrimination tasks, succeed in a reversal task
482 and probably retain some information about a previously learned task when
483 progressing to a new one. Apart from distinguishing between different visual stimuli,
484 several studies have investigated electroreceptive discrimination abilities of sharks and
485 rays. Electroreception is involved in a range of behaviours but seems to be of particular
486 importance to benthic species when hunting for buried or camouflaged prey (Tricas
487 and Sisneros 2004). Kimber et al. (2011) tested if small-spotted catsharks
488 (*Scyliorhinus canicula*) could not only detect electric fields (as had been shown

489 previously) but discriminate between prey-type electric fields, and how these sharks
490 react to artificial electric fields compared to natural ones. Sixty six sharks were trained
491 to swim through a tunnel and choose then between two electric fields. Several options,
492 consisting of artificial (AC and DC) and natural (DC) electric fields, featuring currents
493 of the same, similar or differing magnitudes were presented. Results indicated that
494 when sharks were provided with two artificial fields with DC currents of different
495 magnitude, they would prefer the stronger one, when presented with a DC current and
496 an AC current of the same magnitude they preferred the AC one, and when presented
497 with a natural and an artificial DC current of similar magnitude they showed no
498 preference, despite the natural current being associated with a food reward. A similar
499 study was conducted by Kimber et al. in 2014, where electroreceptive foraging
500 behaviour was further investigated (see Section 7). Electric dipole polarity, i.e. the
501 discrimination of cathode and anode, was tested in a study by Siciliano et al. (2013) in
502 the yellow stingray (*Urobatis jamaicensis*). Eleven rays were successfully trained within
503 18-22 days to bite either the anode or cathode and in transfer tests discriminated
504 between the poles significantly above chance level. Currently, (visual) object
505 categorization abilities are being tested on bamboo sharks (Schluessel unpublished)
506 and results indicate very similar learning rates and performances as found in cichlids
507 (Schluessel et al. 2012). Categorization is the ability of an animal to combine
508 distinguishable events, objects or items into discrete mental units which are then
509 treated equivalently (Mervis and Rosch 1981). Similarities among such events, objects
510 and items are recognized and categories constructed that symbolize shared features
511 (Spinozzi 1996). This ability can be used for a wide variety of behaviours such as to
512 identify new objects, solve problems, communicate ideas and obtain environmental
513 information (Spinozzi 1996). Categorization abilities have also been shown for sharks
514 in a study assessing symmetry perception, discussed in Section 5 (Schluessel et al.
515 2014).

516
517 Previous studies in teleosts have demonstrated successful visual detection and
518 recognition of 2D as well as 3D shapes (e.g. Herter 1929, 1930; Wyzisk & Neumeyer
519 2007; Siebeck et al. 2009; Schluessel et al. 2012; Gierszewski et al. 2013; Schluessel
520 et al. 2013), as well as discrimination of objects using active electrolocation (von der
521 Emde 1999). Fish, like primates and humans, can categorize (Schluessel et al. 2012;
522 2013) and distinguish images from their mirror image counterparts (Gierszewski et al.

523 2013). No matching-to-sample (MTS) ability was found using geometric symbols in
524 cichlids (Gierszewsky et al. 2013) but it has been successfully shown for goldfish by
525 Goldman and Shapiro (1979) and Zerbolio and Royalty (1983) using colored lights.
526 The visual cues recognized by fish to single out individuals or objects under natural
527 conditions are extremely diverse. Among them are postural changes, subtle as well as
528 distinct colour and shape variations, facial and bodily patterns as well as size
529 differences (Wunder 1934; Karplus & Algom 1981; Karplus et al. 1982; Csanyi 1985,
530 1986; Altbacker and Csanyi, 1990). Several studies on fish have addressed the
531 problem of size constancy (Herter 1930; Douglas et al. 1988; Schuster et al. 2004) and
532 form constancy was recently shown in cichlids by Schluessel et al. (2013). Using its
533 electrosensory system the weakly electric fish *Gnathonemus petersii* displayed rotation
534 invariance and size constancy and there was some indication that it could perceive
535 illusory contours (von der Emde et al. 2010).

536

537 5. Symmetry perception

538 Teleosts and sharks can discriminate symbols and objects and have some ability to
539 categorize these (see Section 4). In this process, certain object features, including
540 colour, edges, size and form may cause animals to prefer one object over another.
541 This can also include symmetry. Mammals including humans, birds and many other
542 vertebrates as well as invertebrates, show an ability to perceive or even prefer
543 symmetrical structures. For once, symmetry may be used as a measure of superior
544 genetic quality, i.e. animals which display highly symmetrical features are perceived
545 as more attractive than those that show less symmetrical ones, owing to the fact that
546 a healthy or good genotype is signalled by a symmetrical phenotype (e.g. Leung and
547 Forbes 1996). Additionally, symmetry may influence the selection of food sources
548 (Rodriguez et al. 2004). Until recently, symmetry perception in teleosts had mainly
549 been tested in the context of sexual selection; in case of Cortez swordtails for example,
550 females prefer males displaying an equal number of vertical stripes on either side
551 (Morris and Casey 1998; Merry and Morris 2001), while female three-spined
552 sticklebacks show a significant preference for males featuring symmetrically arranged
553 pectoral fins (Mazzi et al. 2003; Mazzi et al. 2004). However, not all fish species
554 necessarily have a preference for symmetry or at least regularity; Rensch (1957; 1958)
555 and Tigges (1962) for example showed that the cichlid *Cichlasoma biocellatum*
556 preferred irregular over regular stimuli. Schluessel et al (2014) comparatively assessed

557 whether cichlids (*Pseudotropheus* sp.) and bamboo sharks (*Chiloscyllium griseum*),
558 could distinguish symmetry from asymmetry independent of a specific biological
559 context (such as mating behaviour). In two alternative forced choice experiments,
560 individuals were tested for spontaneous preferences and trained to discriminate
561 between abstract symmetrical and asymmetrical stimulus pairs (Figure 3). Pair
562 discriminations were followed by extensive categorization experiments (new symbols
563 being presented on each trial) once individuals had solved the former successfully
564 (Figure 3). By testing individuals for their ability to categorize symmetrical from
565 asymmetrical symbols the possibility that individual stimulus pairs were only
566 distinguished based on single elementary features, such as edges, lines or the
567 arrangement of light and dark segments was eliminated. In the categorization
568 experiments each individual was exposed to a completely new pair of stimuli on each
569 trial, thereby making it impossible to choose correctly based on any other feature than
570 the one tested for (the only constant), in this case symmetry. Both sharks and cichlids
571 are bilaterally symmetric organisms and fluctuating asymmetries in various bodily
572 features could potentially act as indicators for genetic quality despite the absence of
573 any obvious symmetrical body markings in either species. While sharks showed both
574 a significant spontaneous preference for symmetry as well as remarkable
575 discrimination abilities by succeeding in all of the presented tasks, cichlids showed no
576 spontaneous preference, had difficulties in discriminating between symbols and
577 performed poorly in the categorization experiments. Sharks could also distinguish
578 between bilaterally and rotationally symmetrical stimuli. These results indicate that the
579 degree of symmetry perception varies significantly between the two species and to a
580 lesser extent between individuals. Obviously, performance depends on the types of
581 stimuli used and their relevance to the respective organism being tested, so potentially
582 the cichlids might have performed better if other stimuli had been used. The fact that
583 sharks, and to some extent possibly even cichlids, possess a symmetry concept
584 provides further evidence for the parallels and similarities between the mammalian
585 (including human) and the fish visual system and visual information processing.
586 Another example for this is given in the following section on the perception of illusory
587 contours.

588

589

590

591 6. Illusory contours

592 The visual systems of many vertebrates and even invertebrates perceive illusory
593 contours despite the absence of physical luminance, colour or textural differences.
594 Illusory contours are 'misreadings' of visual information by the brain; instead of just
595 processing the actual information coming from the retina, the brain adheres to
596 preconceptions and assumes what is most likely to be seen, based on previous
597 experiences and neural wiring (Kandel et al. 2000). This is just one of many examples
598 that indicate that vision is a creative process in which different pieces of information
599 are processed according to system specific rules (Kandel et al. 2000). The most
600 famous examples of such phenomena are provided by several optical illusions called
601 the 'Kanizsa figures', which are produced when the brain is fooled into seeing a square
602 or a triangle, without there actually being a physical counterpart (Kanizsa 1974). Other
603 examples are Müller-Lyer illusions, subjective contours and various forms of amodal
604 completion. Several studies have already shown that teleosts can be deceived by
605 optical illusions (e.g. Agrillo et al. 2013, Nieder 2002), perceive illusory contours such
606 as Kanizsa figures (Wyzisk 2005; Wyzisk and Neumeier 2007), and can recognize
607 partly occluded or fragmented objects (Sovrano and Bisazza 2008; 2009; Darmaillacq
608 2011). Very recently, a review on illusory contours in teleosts was published by Agrillo
609 et al. (2013), pointing out the similarities between various vertebrate systems in this
610 respect. Bamboo sharks (*Chiloscyllium griseum*) have been tested for their ability to
611 perceive subjective and illusory contours (Fuss et al. 2014d) and just like teleosts and
612 other vertebrates were found to fall for most common illusions, but not for all. Sharks
613 were first trained to recognize an empty square as the positive, rewarded stimulus over
614 a filled square, which was not rewarded when chosen. As soon as the learning criterion
615 was reached, transfer tests were conducted to test if sharks preferentially chose a
616 Kanizsa square over seven different randomized Pacman figures. In a second step an
617 empty square as the positive, rewarded stimulus had to be distinguished from an empty
618 triangle. Following successful training, sharks were presented with a series of transfer
619 tests to determine whether the Kanizsa figure resembling the positive training stimulus
620 (square) was chosen over an alternative one (triangle). In both experiments the correct
621 stimulus was chosen significantly often over the alternative one, indicating that sharks
622 were perfectly able to recognize and distinguish between Kanizsa figures (Figure 4).
623 In a second experiment, it was tested whether grating gaps and phase shifted abutting
624 gratings could also be perceived and distinguished. Sharks were first trained to choose

625 a white square presented on diagonal lines against a rhomboid. Following successful
626 training, sharks were again presented with subjective contours in a series of transfer
627 tests. During these, sharks successfully chose a subjective contour of a square (using
628 grating gaps within the white lines) over a rhomboid and successfully chose a
629 subjective contour of a square (using phase-shifted abutting gratings) over the
630 subjective contour defining a rhomboid. However, unlike most humans and several
631 other species, sharks were not deceived by Müller-Lyer illusions. In these, two centre
632 lines of equal length are comparatively set between two arrowheads or –tails, in which
633 case the line featuring the two arrow tails appears to be longer to most humans,
634 primates and birds, but not to teleosts and as it turns out also not to sharks. In
635 preparation for this experiment, lines of varying length, and lines of unequal length
636 randomly featuring either two arrowheads or -tails on their ends, were presented first
637 and were successfully distinguished by most sharks. During presentation of the Müller-
638 Lyer illusions sharks succumbed either to side preferences or chose according to
639 chance. Interestingly, Müller-Lyer illusions are generally one of the ‘weaker’ illusions,
640 to which also humans have very varying reactions, i.e. Europeans for example are
641 more susceptible to it than more traditional cultures such as Inuits or Aborigines (Berry,
642 1968; Segall et al. 1966). Results clearly show that visual perception is a creative
643 process, not just for humans but seemingly for all vertebrates and most likely
644 invertebrates as well. The system specific rules leading to the recognition of illusory
645 contours seem to be the same across distantly related groups and results thereby
646 provide information on the evolutionary origin and development of selected cognitive
647 abilities and the characteristics of shared or non-shared neural mechanisms.

648

649 7. Memory retention

650 Memory windows in fish vary greatly between species and tasks (Brown 2001), i.e. not
651 all learned information is retained for equal amounts of time. In some cases it may be
652 advantageous for an animal to forget particular behaviours quickly to retain flexibility
653 (Warburton, 2003) while potentially life-saving behaviour should be retained for longer
654 periods of time or even indefinitely. For example, retaining spatial memory information
655 may be useful if a fish remains within a spatially complex but stable habitat (Odling-
656 Smee et al. 2008) or alternates between places, but less beneficial for fish occupying
657 unstable or rapidly changing habitats, such as fast-flowing rivers (Odling-Smee and
658 Braithwaite 2003). Similarly, information on food patch profitability and temporary prey

659 types may change frequently and should therefore only be remembered on a short-
660 term basis as well (Warburton 2003). Also, the rate at which animals remember the
661 learned information decreases exponentially with time (White, 2001), and more
662 recently acquired information is usually the most important and therefore remembered
663 best (Cuthill et al. 1990). Early experiments showed that lemon sharks retain the
664 memory of how to obtain food in an instrumental conditioning paradigm for up to ten
665 weeks (Clark 1959); however, this was only based on a single observation. Recently,
666 Schluessel and Bleckmann (2012) trained grey bamboo sharks (*Chiloscyllium*
667 *griseum*) in two different spatial tasks (place procedure and turn procedure) and tested
668 whether individuals could still solve the task after an absence of reinforcement of 5,
669 16, 21 and 41 days. All sharks were successful in remembering what they had been
670 trained in up to the maximally tested break period of six weeks. However, it is quite
671 likely that sharks could have remembered the tasks for much longer as indicated by
672 several other experiments (Fuss and Schluessel pers observ.). These give reason to
673 believe that sharks can easily remember discrimination tasks using abstract geometric
674 or symmetrical symbols for several months. Guttridge and Brown (2014) trained Port
675 Jackson sharks (*H. portjacksoni*) in several classical conditioning paradigms, pairing a
676 LED light or a stream of air bubbles with a food reward, using a delay, a trace and a
677 control procedure. While all animals learned the task irrespective of the procedure
678 used, performance varied significantly between these. Overall, results indicated that
679 sharks Port Jackson sharks can relate two time-separated events and the retention of
680 learned associations for a period of at least 24 hours but possibly even up to 40 days.
681 Another study was conducted by Kimber et al. (2014) who used electroreceptive
682 foraging in the small-spotted catshark, *Scyliorhinus canicula*, to test learning and
683 memory abilities. As shown in previous studies using visual or electrical stimuli (e.g.
684 Fuss et al. 2014c; Schluessel et al. 2014; Kimber et al. 2011; Siciliano et al. 2013),
685 sharks learned quickly to locate and acquire a food reward associated with an artificial
686 electric field, and rewarded cat sharks showed more interest in electrodes than
687 unrewarded ones, which habituated and finally ceased to respond to the electrodes
688 altogether. Individuals were only trained twice a day for five days, so overall sharks
689 learned very quickly to respond maximally to profitable stimuli but also to quickly
690 habituate to non-profitable ones, thereby maximizing resources. None of the learned
691 and habituated behaviors were remembered after a three week interval without
692 reinforcement, indicating that the memory window for such a task must lay between

693 twelve hours (as sharks remembered the task on consecutive days) and less than three
694 weeks. The authors concluded that ‘forgetting’ in regards to foraging behavior may
695 actually provide an advantage for an opportunistic benthic predator such as the small-
696 spotted catshark living in a variable environment in which resources are likely to be
697 distributed patchy (Kimber et al. 2014). Similar suggestions have also been raised by
698 Warburton working on food patch profitability in teleosts (2003). While food-related
699 behavior may not be remembered for long due to the variability of food sources and
700 alteration of environmental variables, it would be beneficial to remember possibly life-
701 threatening behavior for extended periods of time, if not indefinitely. Surprisingly, no
702 such skill was found in juvenile lemon sharks, which were tested for the ability to avoid
703 getting hooked on long-line equipment based on their ability to detect electric fields
704 (Spaet et al. 2010). Six individuals were trained to distinguish between a plastic and a
705 metal hook; when attempting to take bait from the former, sharks remained
706 undisturbed, while feeding from the metal hook resulted in a mechanical penalty.
707 Neither significant learning nor the retention of learned information regarding the
708 discrimination of hooks was observed.

709

710 As mentioned previously, studies on teleosts indicate that fish can possess quite
711 extensive long-term memories (Brown 2001; Warburton 2003), for example escape
712 responses were retained for eleven months (Brown 2001), while hook avoidance
713 reactions lasted for over a year (Tarrant 1964; Beukema 1970). Information on
714 successful feeding locations and social cooperations usually were remembered less
715 well, in the order of weeks (Dugatkin and Wilson 1992). Associations of time-separated
716 events as well as spatial information are remembered for several month to about half
717 a year (Fricke 1974; Bshary et al. 2002; Fukumori et al. 2009). However, other
718 information regarding spatial memory may be lost sooner, after only days or a few
719 weeks (Goldsmith 1914; Aronson 1951, 1971). Information on foraging was also
720 forgotten at different rates depending on skill and species, in some cases newly
721 acquired feeding information was completely forgotten after only days (e.g. Croy and
722 Hughes 1991), while a few memories lasted up to several months (Ware 1971).

723

724

725

726

727 8. Avoidance learning

728 In the past decades, classical conditioning of avoidance behaviour has been
729 investigated in a range of teleost and elasmobranch species. For aversive conditioning
730 the neutral-discriminative stimuli combination can involve various sensory modalities,
731 e.g. an acoustic tone, an olfactory cue or a visual (light) cue paired with an electric
732 stimulus. Different behavioural reactions in response to an aversive stimulus have
733 been observed as for example higher or lower heart frequency (Kelly and Nelson 1975;
734 Rodríguez et al. 2005), shivering (Chandroo et al. 2004; Sanders et al. 2003), inactivity
735 (e.g. Bindra and Anchel 1963; Jackson et al. 1980), or an escape reaction (e.g.
736 Portavella et al. 2002; Yue et al. 2004). In an earlier investigation, Nelson (1967)
737 showed that sharks (*Negaprion brevirostris*) could be conditioned to different acoustic
738 frequencies using aversive stimuli. Another study investigated if magnetic fields could
739 act as aversive stimuli to sharks by using magnetic fields as barriers, simulating beach
740 nets (O'Connell et al. 2011). Schwarze et al. (2013) tested whether bamboo sharks
741 (*Chiloscyllium griseum*, *C. punctatum*) and coral cat sharks (*Atelomycterus*
742 *marmoratus*) could be conditioned in a classical conditioning paradigm, pairing a mild
743 electric stimulus with a visual stimulus in form of a green light. Seven out of twelve
744 individuals were successfully conditioned; unfortunately though, sharks did not show
745 an escape response as previously observed on goldfish. Instead, individual specific
746 responses such as backwards swimming or head movements. As opposed to previous
747 classical conditioning studies on elasmobranchs, behavioural trials were subsequently
748 complemented by neuroanatomical assessment, to investigate the influence of the
749 telencephalon on the processing of aversion learning.

750

751 Several studies have tried to identify those parts of the brain involved in or responsible
752 for avoidance responses in teleosts. All have implicated the telencephalon (reviewed
753 in Rodríguez et al. 2006). It has also been shown that a part of the medial pallium in
754 teleost fish is homologous to the amygdala in land vertebrates (e.g. Portavella et al.
755 2002 Portavella and Vargas 2005; Vargas et al. 2009). Like the hippocampus, the
756 amygdala is a limbic system structure involved in certain aspects of learning and
757 memory, specifically in emotionally related aspects (e.g. Maren and Holt 2004; Squire
758 2004). These studies demonstrated that after lesions of the medial pallium goldfish
759 were unable to show a previously learned avoidance reaction in a classical
760 conditioning task. Selected lesion studies have also tried to match telencephalic brain

761 regions to different behaviours of nurse sharks (*Ginglymostoma cirratum*) (Graeber et
762 al. 1978; Graeber 1978; 1980) and in contrast to studies on teleosts it has been claimed
763 that visual impairments follow telencephalon ablation (Graeber et al. 1978). Schwarze
764 et al. (2013) removed most of the pallial region within the telencephalon to test if this
765 would impair avoidance learning and fear conditioning in the bamboo shark. In sharks,
766 the equivalent to the teleost medial pallium would probably be situated in a region
767 lateroventral of the lateral pallium and dorsolateral of the area superficialis basalis
768 (pers. comm. M. Wullimann). Naive individuals were either trained and then
769 telencephalon lesioned or first lesioned and then trained, to determine, whether
770 removal of the pallium would disrupt the retrieval of a previously learned task and/or
771 inhibit the learning of a new task. Two out of four sharks in the first group reached the
772 learning criterion again after surgery within 8 and 9 sessions, respectively. However,
773 despite performing above the learning criterion, the sharks were less successful and
774 slower after surgery than before. All three sharks that were lesioned prior to training
775 were successfully conditioned in about the same number of sessions. However,
776 histological analysis showed that the lesions of these sharks were much smaller than
777 the lesions of sharks that were first trained and then operated on. The two animals that
778 were not able to solve the task after surgery showed the greatest lesions overall and
779 in contrast to the other sharks featured much larger damage in the dorsolateral areas.
780 This indicates that the lateroventral regions of the lateral pallium and regions close to
781 the subpallial area superficialis basalis may indeed be the structures involved in
782 avoidance learning in elasmobranchs. Additional control mechanisms for the learned
783 behaviour could also be provided by other brain areas (e.g. cerebellum) (Flood et al.
784 1976; Hofmann 2001).

785

786 Conclusions

787 Even in the absence of overwhelming experimental evidence, for a complex organism
788 the success of persisting for over 450 Million years should provide some support for
789 the presence of cognitive abilities which, just like any other trait, are subject to
790 evolutionary selection pressures. Fortunately, in recent years increasing numbers of
791 studies have started to investigate this topic more closely and finally provided some
792 experimental evidence for what in my view seemed highly likely anyway, i.e. that
793 elasmobranchs share cognitive skills found in teleosts and other vertebrates. The
794 present review has compiled the currently available data and tried to highlight the

795 diverse aspects of cognitive functions found in this ancient vertebrate group in
796 comparison to teleosts, which have been studied in much greater detail. While there is
797 obviously still a wide open field for further investigations, these pilot studies have
798 shown that sharks and rays can learn and habituate, possess spatial memory and can
799 orient according to different strategies, remember spatial tasks for extended periods of
800 time, use tools, can imitate and learn from others, can distinguish between conspecifics
801 and heterospecifics, discriminate between objects using vision and electroreception,
802 can categorize visual objects and perceive illusory contours as well as symmetry
803 (including distinguishing between bilateral and point symmetry). As in teleosts, a very
804 large ratio of behavioural compared to neuroanatomical studies assessing cognition
805 exists in elasmobranchs, and with few exceptions (Sections 1 and 8) this review has
806 had to focus solely on the former. Hopefully, this may change in the future as identifying
807 the neural substrates which underlie cognitive functions is an extremely interesting field
808 for which many techniques are available, including neuroanatomical techniques (tract-
809 tracing, intracellular labelling, specific neuropharmacological blocking/activation and
810 selective lesion studies), neurophysiological methods (evoked potentials and single
811 cell recordings as well as optical recordings) and gene expression patterns (immediate
812 early gene analysis). Behavioural studies are often hard to conduct and results are
813 sometimes ambiguous or to be regarded with caution. Data obtained in the laboratory
814 are not always representative of what occurs in the wild and similarly, conditions in the
815 field are often so difficult to control – if not uncontrollable - that there is rarely a
816 guarantee that all possible confounding factors have been eliminated. Sharks, or at
817 least their behaviour and cognitive skills, are specifically hard to study, as many
818 species are free ranging, hard to maintain in captivity and massive in size. Obviously,
819 the ecological significance of the stimulus to be tested should always be taken into
820 consideration, because if a test has no ecological relevance it may not be surprising if
821 the animal performs below expectations. Owing to the difficulty of obtaining and
822 maintaining sharks in a laboratory or creating controllable experimental conditions in
823 the field, finding a suitable stimulus may not be possible, or at least may prove to be
824 very challenging. Testing of abstract stimuli (out of an ecological context) can still be
825 used to show if a certain ability is present. If the animal responds and positive results
826 are obtained, the stimuli are obviously sufficient despite their artificiality. However, if
827 the animal does not respond to these stimuli or results are not significant, one cannot
828 conclude that the ability to be tested is not present in the animal; it may simply be the

829 inappropriate stimulus precluding proper results. Most of the previously tested abilities
830 in elasmobranchs have some relevance to natural conditions; one could expect sharks
831 living in complex environments such as coral reefs, or territorial species, to have some
832 form of spatial memory, memory retention as well as certain visual discrimination or
833 categorization abilities if they are able to find and remember hiding places and food
834 patches and to recognize and remember con-specifics, predators and prey. Juvenile
835 sharks are subject to higher predation rates at dusk or dawn, and may find more food
836 at specific times during the tidal cycle or during the day, so the ability for spatiotemporal
837 learning would provide benefits in regards to foraging efficiency or successful predator
838 avoidance. Relying on global spatial cues instead of local cues (beacons) provides for
839 more flexibility, as individual landmarks may disappear, become obscured from view,
840 deteriorate or simply change appearance. However, some other tests may not seem
841 to be immediately very relevant, as for example the perception of very artificial
842 symmetrical symbols or deception by illusory contours, but these nonetheless present
843 nice examples of parallel information processing in such distantly related organisms
844 as humans and sharks. While the cognitive abilities of some elasmobranchs like the
845 white shark (*Carcharodon carcharias*) or the blue shark (*Prionace glauca*) may always
846 remain elusive due to their life styles, relative inaccessibility and the inability to be
847 maintained in a laboratory, I am quite certain that future studies will elucidate many
848 more fascinating aspects of the previously rather neglected cognitive abilities within
849 this group.

850

851 Acknowledgements

852

853 I am grateful to H. Bleckmann and M. Mogdans for helpful suggestions on the
854 manuscript.

855

856

857

858

859

860

861

862

863

864

865 Literature

866

867 Agrillo C, Petrazzini MEM, Dadda M. (2013). Illusionary patterns are fishy for fish, too.
868 Front Neural Circuits 7:137. doi: 10.3389/fncir.2013.00137

869

870 Altbacker V, Csanyi V (1990) The role of eyespots in predator recognition and
871 antipredatory behavior of the paradise fish, *Macropodus-opercularis*. L Ethol 85: 51-57

872

873 Aronson LR (1951) Orientation and jumping behavior in the gobiid fish, *Bathygobius*
874 *soporator*. Am Mus Novit 1486:1–22

875

876 Aronson LR (1971) Further studies on orientation and jumping behaviour in the gobiid
877 fish, *Bathygobius Soporator*. In: Adler HE (ed) Orientation: sensory bases. Ann NY
878 Acad Sci 188:378–392

879

880 Aronson LR, Aronson FR, Clark E (1967) Instrumental conditioning and light-dark
881 discrimination in young nurse sharks. Bull Mar Sci 17: 249-56

882

883 Atoji Y, Wild JM, (2006) Anatomy of the avian hippocampal formation. Rev Neurosci
884 17: 3–16

885

886 Banner A (1972) Use of sound in predation by young lemon sharks, *Negaprion*
887 *brevirostris* (Poey). Bull Mar Sci 22:251–283

888

889 Beukema JJ (1970) Angling experiments with carp (*Cyprinus carpio* L.) II. Decreasing
890 catchability through one-trial learning. Neth J Zool 20:81–92

891

892 Berry JW (1968) Ecology, perceptual development and the Muller-Lyer illusion. *British*
893 *J Psychol* 59: 205-210.

894

895 Bindra D, Anchel H (1963) Immobility as an avoidance response, and its disruption by
896 drugs. J Exp Anal Behav 6:213–8.

897

898 Brown C, Laland K, Krause J (2011) Fish cognition and behavior, 2 edn. Blackwell
899 Publishing Ltd, Oxford
900
901 Bshary R, Wickler W, Fricke H (2002) Fish cognition: a primate's eye view. *Anim Cogn*
902 5:1-23
903
904 Bshary R (2006) Machiavellian intelligence in fishes. In: *Fish cognition and behavior*
905 (eds C. Brown, K. Laland and J. Krause). Blackwell Scientific, Oxford, pp. 223–242.
906
907 Brown C (2012) Tool use in fishes. *Fish Fisher* 13: 105-115.
908
909 Butler AB, Reiner A, Karten HJ (2011) Evolution of the amniote pallium and the origins
910 of mammalian neocortex. *Ann N Y Acad Sci* 1225: 14-27
911
912 Chandroo K, Duncan IJ, Moccia R (2004) Can fish suffer?: perspectives on sentience,
913 pain, fear and stress. *Appl Anim Behav Sci* 86:225–250.
914
915 Chittka L, Skorupski P (2011) Information processing in miniature brains. *Proc R Soc*
916 B 278: 885-888
917
918 Clark E (1959) Instrumental conditioning of lemon sharks. *Science* 130: 217-18.
919
920 Clark E (1961) Visual discrimination in lemon sharks. Tenth Pacific Science Congress,
921 Honolulu. 10: 175-176
922
923 Clark E (1963) The maintenance of sharks in captivity, with a report on their
924 instrumental conditioning. In: Gilbert PW (ed) *Sharks and survival*. DC Heath,
925 Boston, pp 115-50
926
927 Compagno LJV (1999) Systematics and body form. In: Hamlett WC (ed) *Sharks,*
928 *skates, and rays: The biology of elasmobranch fishes*. Johns Hopkins University Press,
929 Baltimore, pp 1-42
930

931 Coolen I, Bergen YV, Day RL, Laland KN (2003) Species difference in adaptive use of
932 public information in sticklebacks. Proc R Soc Lond B 270: 2413-2419
933

934 Costa SS, Andrade R, Carneiro LA, Goncalves EJ, Kotrschal K, Oliveira RF (2011)
935 Sex differences in the dorsolateral telencephalon correlate with home ranges in
936 blenniid fish. Brain Behav Evol 77: 55-64
937

938 Coyer J (1995) Use of a rock as an anvil for breaking scallops by the yellowhead
939 wrasse, *Halichoeres garnoti* (Labridae). Bull Mar Sci 57: 548–549.
940

941 Croy MI, Hughes RN (1991) The role of learning and memory in the feeding behaviour
942 of the fifteen-spined stickleback, *Spinachia spinachia* L. Anim Behav 41:149–159.
943

944 Csanyi V (1985) Ethological analysis of predator avoidance by the paradise fish
945 (*Macropodus-opercularis* L). 1. Recognition and learning of predators. Behav 92: 227-
946 240
947

948 Csanyi V (1986) Ethological analysis of predator avoidance by the paradise fish
949 (*Macropodus-opercularis* L). 2. Key stimuli in avoidance-learning. Anim Learn Behav
950 14: 101-109
951

952 Cuthill IC, Kacelnik, A, Krebs JR, Haccou P, Iwasa Y (1990) Starlings exploiting
953 patches: the effect of recent experience on foraging decisions. Anim Behav 40: 625-
954 640
955

956 Darmaillacq AS, Dickel L, Rahmani N, Shashar N (2011). Do reef fish, *Variola louti* and
957 *Scarus niger*, perform amodal completion? Evidence from a field study. J Comp
958 Psychol 125:273
959

960 Demski LS (2013) The pallium and mind/behavior relationships in teleost fishes. Brain
961 Behav Evol 82: 31-44
962

963 Desjardins JK, Fernald RD (2011) What do fish make of mirror images? *Biol Lett* 6:
964 744-747
965 Dicke U, Roth G (2007) Evolution of the amphibian nervous system. In: Kaas
966 JH (ed) *Evolution of Nervous Systems, Vol 2*. Academic Press, Oxford, pp 61-124
967
968 Dittman AH, Quinn TP (1996) Homing in Pacific salmon: mechanisms and ecological
969 basis. *J Exp Biol* 199: 83–91.
970
971 Douglas RH, Eva J, Guttridge N (1988) Size constancy in goldfish (*Carassius auratus*).
972 *Behav Brain Res* 30: 37–42.
973
974 Dugatkin LA (1992) Sexual selection and imitation: females copy the mate choice of
975 others. *Am Nat* 139: 1384-1389
976
977 Dugatkin LA, Wilson DS (1992) The prerequisites of strategic behavior in the bluegill
978 sunfish. *Anim Behav* 44: 223–30
979
980 Durán E, Ocana FM, Gómez A, Jiménez-Moya F, Broglio C, Rodríguez F (2008)
981 Telencephalon ablation impairs goldfish allocentric spatial learning in a “hole-board”
982 task. *Acta Neurobiol Exp* 68: 519–25
983
984 Durán E, Ocana FM, Broglio C, Rodríguez F, Salas C (2010) Lateral but not medial
985 telencephalic pallium ablation impairs the use of goldfish spatial allocentric strategies
986 in a “hole-board” task. *Behav Brain Res* 214: 480-487
987
988 Ebbesson SOE (1972) New insights into the organization of the shark brain. *Comp*
989 *Biochem Physiol* 42: 121–129
990
991 Ebbesson SOE (1980) On the organization of the telencephalon in elasmobranchs. In:
992 Ebbesson SOE (ed) *Comparative neurology of the telencephalon*. Plenum Press, New
993 York, pp 1–16
994
995 Ebbesson LOE, Braithwaite VA (2012) Environmental effects on fish neural plasticity
996 and cognition. *J Fish Biol.* 81: 2151-2174

997 Economakis AE, Lobel PS (1998) Aggregation behavior of the grey reef shark,
998 *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. Environ Biol
999 Fish 51: 129-139
1000
1001 Edren SMC, Gruber SH (2005) Homing ability of young lemon sharks, *Negaprion*
1002 *brevirostris*. Environ Biol Fish 72, 267-281
1003
1004 Ferreira TL, Moreira KM, Ikeda DC, et al. (2003) Effects of dorsal striatum lesions in
1005 tone fear conditioning and contextual fear conditioning. Brain Res 987:17–24
1006
1007 Finger T (2008) Sorting food from stones: the vagal taste system in goldfish, *Carassius*
1008 *auratus*. J Comp Physiol A 194:135-143
1009
1010 Flood NC, Overmier JB, Savage GE (1976) Teleost telencephalon and learning: an
1011 interpretive review of data and hypotheses. Physiol Behav 16:783–798.
1012
1013 Font E, García-Verdugo JM, Desfilis E, Pérez-Cañellas M (1995) Neuron-glia
1014 interrelations during 3-acetylpyridine-induced degeneration and regeneration in the
1015 adult lizard brain. In: Vernadakis A, Roots B (eds) Neuron-glia interrelations during
1016 phylogeny: II. Plasticity and regeneration. Humana, Totowa, NJ, pp 275–302.
1017
1018 Fricke H (1971) Fische als Feinde tropischer Seeigel. Mar Biol 9: 328–338.
1019
1020 Fuss T, Bleckmann H, Schluessel V (2014a) Place learning prior to and after
1021 telencephalon ablation in bamboo and coral cat sharks (*Chiloscyllium griseum* and
1022 *Atelomycterus marmoratus*). J Comp Physiol A 200:37-52
1023
1024 Fuss T, Bleckmann H, Schluessel V (2014b) The shark *Chiloscyllium griseum* can
1025 orient using turn responses before and after partial telencephalon ablation. J Comp
1026 Physiol A 200:19-35
1027
1028 Fuss T, Bleckmann H, Schluessel V (2014c) Visual discrimination abilities in grey
1029 bamboo sharks (*Chiloscyllium griseum*). Zool 117: 104-111

1030 Fuss T, Bleckmann H, Schluessel V (2014d) The brain creates illusions not just for us:
1031 turns out sharks (*Chiloscyllium griseum*) can 'see the magic' as well. Front Neural
1032 Circuits 8: 24. doi: 10.3389/fncir.2014.00024
1033

1034 Fukumori K, Okuda N, Yamaoka K, Yanagisawa Y (2009) Remarkable spatial memory
1035 in a migratory cardinal fish. Anim Cogn 13:385-389
1036

1037 Gierszewski S, Bleckmann H, Schluessel V (2013) Cognitive abilities in Malawi cichlids
1038 (*Pseudotropheus* sp.): Matching-to-sample and image/mirror-image discriminations.
1039 PLoS One 8: e57363
1040

1041 Giurfa M (2013) Cognition with few neurons: higher-order learning in insects. T
1042 Neurosci 36: 285–294
1043

1044 Goldman M, Shapiro S (1979) Matching-to-sample and oddity-from-sample in goldfish.
1045 J Exp Anal Behav. 31: 259-266
1046

1047 Graeber RC (1978) Behavioral studies correlated with central nervous system
1048 integration of vision in sharks. In: Hodgson ES, Mathewson RF (eds) Sensory biology
1049 of sharks, skates, and rays. Arlington VA, Office of Naval Research, pp 195-226
1050

1051 Graeber RC (1980) Telencephalic function in elasmobranchs, a behavioral
1052 perspective. In: Ebbesson SOE (ed) Comparative Neurology of the Telencephalon.
1053 Plenum Press, New York, pp 17-39
1054

1055 Graeber RC, Schroeder DM, Jane JA, Ebbesson SOE (1978) Visual discrimination
1056 following partial telencephalic in nurse sharks (*Ginglymostoma cirratum*). J Comp
1057 Neurol 180: 325-344
1058

1059 Grill HJ, Norgren R (1978) Neurological tests and behavioral deficits in chronic thalamic
1060 and chronic decerebrate rats. Brain Res 142: 299-312
1061

1062 Griffith SW, Ward AJW (2006) Learned recognition of conspecifics. In: Brown C, Laland
1063 K, Krause J (eds) Fish cognition and behaviour. Blackwell Publishing Ltd, Oxford, pp
1064 139-165

1065 Griffith SW, Magurran AE (1997) Familiarity in schooling fish: how long does it take to
1066 acquire? *Anim Behav* 945-949

1067

1068 Grosenick L, Clement TS, Fernald RS (2007) Fish can infer social rank by observation
1069 alone. *Nature* 445: 429-432

1070

1071 Gruber SH, Cohen JL (1978) Visual systems of the elasmobranchs: state of the art
1072 1960-1975. In: Hodgson ES, Mathewson RF (eds) Sensory biology of sharks, skates,
1073 and rays. US Government Printing Office, Washington DC, pp 11-116

1074

1075 Gruber SH and Schneiderman N (1975) Classical conditioning of the nictitating
1076 membrane response of the lemon shark (*Negaprion brevirostris*). *Behav Res Meth*
1077 *Instrum* 7: 430-34

1078

1079 Guttridge TL, Gruber SH, Gledhill KS, Croft DP, Sims DW, Krause J (2009) Social
1080 preferences of juvenile lemon sharks *Negaprion brevirostris*. *Anim Behav* 78: 543–548

1081

1082 Guttridge TL, Myrberg AM, Porcher IF, Sims DM, Krause J (2010) The role of learning
1083 in shark behavior. *Fish Fisheries* 10: 450–469

1084

1085 Guttridge TL, Gruber SH, DiBattista JD, Feldheim KA et al (2011) Assortative
1086 interactions and leadership in a wild population of juvenile lemon sharks. *Mar Eco Prog*
1087 *Ser* 423:235–245

1088

1089 Guttridge TL, van Dijk S, Stamhuis EJ, Krause J, Gruber SH, Brown C (2013) Social
1090 learning in juvenile lemon sharks *Negaprion brevirostris*. *Anim Cogn* 16: 55–64

1091

1092 Guttridge TL, Brown C (2014) learning and memory in the Port Jackson shark,
1093 *Heterodontus portusjacksoni*. *Anim Cogn* 17: 415-425

1094

1095 Heiligenberg W (1986) Jamming avoidance responses. In: Bullock TH, Heiligenberg
1096 W (eds) Electroreception. John Wiley and Sons, New York:, pp 613-649
1097
1098 Helfman GS, Schulz ET (1984) Social transmission of behavioral traditions in a coral-
1099 reef fish. Anim Behav 32: 379-38
1100
1101 Herold C, Joshi I, Chehadi O, Hollmann M, Güntürkün O (2012) Plasticity in D1-like
1102 receptor expression is associated with different components of cognitive processes.
1103 PLoS 7: e36484
1104
1105 Herter K (1929) Dressurversuche an Fischen. Z vergl Physiol 10: 688-711.
1106
1107 Herter K (1930) Weitere Dressurversuche an Fische. Z vergl Physiol 11: 730-748.
1108
1109 Heupel MR, Simpfendorfer CA (2005) Quantitative analysis of aggregation behaviour
1110 in juvenile blacktip sharks. Mar Biol 147: 1239–1249
1111
1112 Hofmann MH (2001) The role of the fish telencephalon in sensory information
1113 processing. In: Kapoor BG, Hara TJ (eds) Sensory biology of jawed fishes: new
1114 insights. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, pp 255–274
1115
1116 Hueter RE, Mann, DA, Maruska, KP, Sisneros JA, Demski LS (2004) Sensory biology
1117 of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR, (eds) Biology of sharks
1118 and their relatives. CRC Press, Boca Raton Florida, pp 325–368
1119
1120 Hughes RN, Blight CM (2000) Two intertidal fish species use visual association
1121 learning to track the status of food patches in a radial maze. Anim Behav 59: 613-621
1122
1123 Jacoby DMP, Busawon DS, Sims DW (2010) Sex and social networking: the influence
1124 of male presence on social structure of female shark groups. Behav Ecol 21: 808-818
1125
1126 Jackson RL, Alexander J, Maier SF (1980) Learned helplessness, inactivity, and
1127 associative deficits: effects of inescapable shock on response choice escape learning.
1128 J Exp Psychol: Anim Behav Proc 6:1–20

1129 Johnsson JI, Akerman A (1999) Watch and learn: preview of the fighting ability of
1130 opponents alters contest behaviour in rainbow trout. *Anim Behav* 56: 771-776

1131 Jones A, Brown C, Gardener S (2011) Tool use in the spotted tuskfish, *Choerodon*
1132 *schoenleinii*. *Coral Reefs* 30: 865

1133

1134 Kaas JH (1987) The organization of the neocortex in mammals - implications for
1135 theories of brain function. *Annu Rev Psychol* 38:129-151

1136

1137 Kandel ER, Schwartz JH, Jessell TM (2000) Principles of neural science. McGraw-
1138 Hill, New York.

1139

1140 Kanizsa G (1974) Contours without gradients or cognitive contours? *Giornale Italiano*
1141 *di Psicologia* 1:93-113

1142

1143 Kaplan H, Aronson LR (1967) Effect of forebrain ablation on the performance of a
1144 conditioned avoidance response in the teleost fish, *Tilapia macrocephala*. *Anim Behav*
1145 15:438–448

1146

1147 Karplus I, Algom D (1981) Visual cues for predator face recognition by reef fishes. *J*
1148 *Comp Ethol* 55: 343-364

1149

1150 Karplus I, Goren M, Algom D (1982) A preliminary experimental-analysis of predator
1151 face recognition by *Chromis-caeruleus* (Pisces, Pomacentridae). *J Comp Ethol* 58: 53-
1152 65

1153

1154 Karten HJ (2013) Neocortical evolution: neuronal circuits arise independently of
1155 lamination. *Curr Biol* 23: R12-5

1156

1157 Keenleyside MHA (1979) Diversity and adaptation in fish behaviour. Springer-Verlag,
1158 Berlin

1159

1160 Kelly JC, Nelson DR (1975) Hearing thresholds of the horn shark, *Heterodontus*
1161 *francisci*. *J Acoustic Soc Am* 58:905–9

1162

1163 Kendal JR, Rendell LR, Pike TW, Laland KN (2009) Nine-spined sticklebacks deploy
1164 a hill-climbing social learning strategy. *Behav Ecol* 20:238–244
1165

1166 Kimber JA, Sims DW, Bellamy PH, Gill AB (2011) The ability of a benthic elasmobranch
1167 to discriminate between biological and artificial electric fields. *Mar Biol* 158:1–8
1168

1169 Kimber JA, Sims DW, Bellamy PB, Gill AB (2014) Elasmobranch cognitive ability: using
1170 electroreceptive foraging behaviour to demonstrate learning, habituation and memory
1171 in a benthic shark. *Anim Cogn* 17: 55-65
1172

1173 Kleerekoper H, Timms AM, Westlake GF, Davy FB, Malar T, Anderson VM (1970) An
1174 analysis of locomotor behaviour of goldfish (*Carassius auratus*). *Anim Behav* 18: 317-
1175 330
1176

1177 Kleerekoper H, Matis I, Gensler P, Maynard P (1974) Exploratory behaviour of goldfish
1178 *Carassius auratus*. *Anim Behav* 22: 124-132
1179

1180 Klimley AP, Nelson DR (1981) Schooling of the scalloped hammerhead shark, *Sphyrna*
1181 *lewini*, in the Gulf of California. *Fish Bull* 79: 356-360
1182

1183 Klimley AP (1993) Highly directional swimming by scalloped hammerhead sharks,
1184 *Sphyrna Lewini*, and subsurface irradiance, temperature, bathymetry, and
1185 geomagnetic-field. *Mar Biol* 117: 1–22
1186

1187 Kotrschal A, Taborsky B (2010) Environmental change enhances cognitive abilities in
1188 fish. *PLoS Biol* 8: e1000351. doi:10.1371/journal.pbio.1000351
1189

1190 Kuba MJ, Byrne RA, Burghardt GM (2010) A new method for studying problem solving
1191 and tool use in stingrays (*Potamotrygon castexi*). *Anim Cogn* 13: 507-513
1192

1193 Laland KN, Williams K (1997) Shoaling generates social learning of foraging
1194 information in guppies. *Anim Behav* 53: 1161-1169
1195

1196 Lee SA, Vallortigara G, Ruga V, Sovrano VA (2012) Independent effects of geometry
1197 and landmark in a spontaneous reorientation task: a study of two species of fish. *Anim*
1198 *Cogn* 15:861–870
1199

1200 Lefebvre L (2013) Brains, innovations, tools and cultural transmission in birds, non-
1201 human primates, and fossil hominins. *Front Hum Neurosci* 7:245.
1202

1203 López JC, Broglio C, Rodríguez F, Thinus-Blanc C, Salas C (1999) Multiple spatial
1204 learning strategies in goldfish (*Carassius auratus*). *Anim Cogn* 2: 109–120
1205

1206 Lopez JC, Broglio C, Rodriguez F, Thinus-Blanc C, Salas C (2000) Reversal learning
1207 deficit in a spatial task but not in a cued one after telencephalic ablation in goldfish.
1208 *Behav Brain Res* 109:91-98
1209

1210 Lucas, J. R., Brodin, A., de Kort, S. R. & Clayton, N. S. (2004) Does hippocampal size
1211 correlate with the degree of caching specialisation? *Proc R Soc Lond. B* 271:
1212 2423–2429
1213

1214 Malyukova IV, Rakich L, Kovachevich N (1983) Conditioned motor reactions in free-
1215 living elasmobranchs and bony fishes. *Neurosci Behav Physiol* 13: 482–485
1216

1217 Maren S, Holt WG (2004) Hippocampus and Pavlovian fear conditioning in rats:
1218 muscimol infusions into the ventral, but not dorsal, hippocampus impair the acquisition
1219 of conditional freezing to an auditory conditional stimulus. *Behav Neurosci* 118:97–110
1220

1221 Martínez-García F, Novejarque A, Lanuza E (2009) The evolution of the amygdala in
1222 vertebrates. In: Kaas J (ed) *Evolutionary neuroscience*. Elsevier, Amsterdam, pp 407-
1223 458
1224

1225 Mathis A, Chivers DP, Smith RJF (1996) Cultural transmission of predator recognition
1226 in fishes: intraspecific and interspecific learning. *Anim Behav* 51: 185-201
1227

1228 Mazeroll AL, Montgomery WL (1995) Structure and organization of local migrations in
1229 brown surgeonfish (*Acanthurus nigrofuscus*). *Ethol* 99: 89-106

1230 Mazzi D, Künzler R, Bakker TCM (2003) Female preference for symmetry in computer-
1231 animated three-spined sticklebacks, *Gasterosteus aculeatus*. Behav Ecol Sociobiol 54:
1232 156–161
1233

1234 Mazzi D, Künzler R, Largiadèr CR, Bakker TCM (2004) Inbreeding affects female
1235 preference for symmetry in computer-animated sticklebacks. Behav Genet 34: 417–24
1236

1237 McManus MW, Johnson CS, Jeffries MM (1984) Training nurse sharks using operant
1238 conditioning. Naval Ocean systems Center Tech Rep No 977
1239

1240 Menzel R (2012) The honeybee as a model for understanding the basis of cognition.
1241 Nat Rev Neuroscience 13: 758-768
1242

1243 Merry, Morris, MR (2001) Preference for symmetry in swordtail fish. Anim Behav 61:
1244 477–479
1245

1246 Mervis CB, Rosch E (1981) Categorization of natural objects. Ann Rev Psychol 32: 89-
1247 115
1248

1249 Meyer CG, Holland K, Papastamatiou YP (2005) Sharks can detect changes in the
1250 geomagnetic field. J Roy Soc Inter 2: 129–130
1251

1252 Meyer CC, Papastamatiou YP, Holland KN (2010) A multiple instrument approach to
1253 quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and
1254 Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. Mar
1255 Biol 157: 1857 -1868
1256

1257 Milinski M, Pflüger D, Kulling D, Kettler R (1990a) Do sticklebacks cooperate
1258 repeatedly in reciprocal pairs. Behav Ecol Sociobiol 27: 17-21
1259

1260 Milinski M, Kuelling D, Kettler R (1990b) Tit for Tat: Sticklebacks (*Gasterosteus*
1261 *aculeatus*) “trusting” a cooperating partner. Behav Ecol 1: 7-11
1262

1263 Moreno N, González A (2006) The common organization of the amygdaloid complex
1264 in tetrapods: new concepts based on developmental, hodological and neurochemical
1265 data in anuran amphibians. Prog Neurobiol 78: 61-90
1266
1267 Moreno N, Gonzalez A (2007). Regionalization of the telencephalon in urodele
1268 amphibians and its bearing on the identification of the amygdaloid complex. Front
1269 Neuroanat 1: 1-12
1270
1271 Morris MR, Casey K (1998) Female swordtail fish prefer symmetrical sexual signal.
1272 Anim Behav 55: 33–9
1273
1274 Mueller T, Guo S (2009) The distribution of GAD67-mRNA in the adult zebrafish
1275 (teleost) forebrain reveals a prosomeric pattern and suggests previously unidentified
1276 homologies to tetrapods. J Comp Neurol 516: 553-568.
1277
1278 Mueller T, Wullimann MF, Guo S (2008) Early teleostean basal ganglia development
1279 visualized by zebrafish Dlx2a, Lhx6, Lhx7, Tbr2 (eomesa), and GAD67 gene
1280 expression J Comp Neurol 507: 1245-57.
1281
1282 Mueller T, Wullimann MF (2009) An evolutionary interpretation of teleost forebrain
1283 anatomy. Brain Behav Evol 74: 30-42
1284
1285 Myrberg AA, Gruber AH (1974) Behavior of bonnethead shark, *Sphyrna tiburo*.
1286 Copeia 1974: 358-374
1287
1288 Myrberg AA, Riggio RJ (1985) Acoustically mediated individual recognitions by a coral-
1289 reef fish (*Pomacentrus-partitus*). Anim Behav 33: 411-416
1290
1291 Nams VO (2006) Detecting oriented movement of animals. Anim Behav 72: 1197–
1292 1203
1293
1294 Nelson DR (1967) Hearing thresholds, frequency discriminations and acoustic
1295 orientation in the lemon shark, *Negaprion brevirostris* (Poey). Bull Mar Sci 17: 741-768
1296

1297 Nieder A (2002) Seeing more than meets the eye: Processing of illusory contours in
1298 animals. *J Comp Physiol A* 188: 249-260
1299

1300 Northcutt, R.G. (1977) Elasmobranch central nervous system organization and its
1301 possible evolutionary significance. *Am Zool* 17: 411–429
1302

1303 Northcutt R (1978) Brain organization in the cartilaginous Fishes. In: Hodgson ES,
1304 Mathewson RF (eds) *Sensory biology of sharks, skates and rays*. Office of Naval
1305 Research, Arlington VA, pp 117–193
1306

1307 Northcutt RG (2011) Do teleost fish possess a homolog of mammalian isocortex? *Brain*
1308 *Behav Evol* 78: 136-138
1309

1310 O’Connell CP, Abel DC, Gruber SH, et al. (2011) Response of juvenile lemon sharks,
1311 *Negaprion brevirostris*, to a magnetic barrier simulating a beach net. *Ocean Coast*
1312 *Manag* 54:225–230
1313

1314 Odling-Smee L, Braithwaite VA (2003a) The role of learning in fish orientation. *Fish*
1315 *Fisher* 4: 235-246
1316

1317 Odling-Smee L, Braithwaite VA (2003b) The influence of habitat stability on landmark
1318 use during spatial learning in the three-spined stickleback. *Anim Behav* 65: 701-707
1319

1320 Odling-Smee LC, Simpson SD, Braithwaite VA (2006) The role of learning in fish
1321 orientation. In: Brown C, Laland K, Krause J (eds) *Fish cognition and behaviour*.
1322 Blackwell, Oxford, pp 166–185
1323

1324 Odling-Smee LC, Bouhman JW, Braithwaite VA (2008) Sympatric species of threespine
1325 stickleback differ in their performance in a spatial learning task. *Behav Ecol Sociobiol*
1326 62: 1935-1945
1327

1328 O’Gower AK (1995) Speculations on a spatial memory for the Port Jackson shark
1329 (*Heterodontus portusjacksoni*) (Meyer) (Heterodontidae). *Mar Freshwater Res* 46:
1330 861-871

1331 O'Keefe J, Nadel L (1978) The hippocampus as a cognitive map. Clarendon Press,
1332 Oxford

1333 Papastamatiou YP, Cartamil DP, Lowe CG, Meyer CG, Wetherbee BM, Holland KN
1334 (2011) Scales of orientation, directed walks and movement path structure in sharks. J
1335 Anim Ecol 80: 864-874

1336

1337 Paško K. (2010) Tool-like behavior in the sixbar wrasse, *Thalassoma hardwicke*
1338 (Bennett, 1830). Zoo Biol 29: 767–773

1339

1340 Pike TT, Kendal JR, Rendell LE, Laland KN (2010) Learning by proportional
1341 observation in a species of fish. Behav Ecol 21: 570-575

1342

1343 Pollen AA, Dobberfuhr AP, Scarce J, Igulu MM, Renn SCP, Shumway CA, Hofmann
1344 HA (2007) Environmental complexity and social organization sculpt the brain in Lake
1345 Tangayikan cichlid fish. Brain Behav Evol 70: 21-39

1346

1347 Portavella M, Vargas JP, Torres B, Salas C (2002) The effects of telencephalic pallial
1348 lesions on spatial, temporal and emotional learning in goldfish. Brain Res Bull 57: 397-
1349 399

1350

1351 Portavella M, Vargas JP (2005) Emotional and spatial learning in goldfish is dependent
1352 on different telencephalic pallial systems. Europ J Neurosci 21: 2800-2806

1353

1354 Puelles L, Kuwana E, Puelles E, Bulfone A, Shimamura K, Keleher J, Smiga S,
1355 Rubenstein JLR (2000) Pallial and subpallial derivatives in the embryonic chick and
1356 mouse telencephalon, traced by the expression of the genes *Dlx-2*, *Emx-1*, *Nkx-2.1*,
1357 *Pax-6*, and *Tbr 1*. J Comp Neurol 424: 409–438

1358

1359 Puelles L, Harrison M, Paxinos G, Watson C (2013) A developmental ontology for the
1360 mammalian brain based on the prosomeric model. T Neurosci 36: 570-578

1361

1362 Reiner A (2004) Avian brain nomenclature consortium. Revised nomenclature for avian
1363 telencephalon some related brainstem nuclei. J Comp Neurol 473: 377-414

1364

1365 Rasmussen LEL, Schmidt MJ (1992) Are sharks chemically aware of crocodiles? In:
1366 Doty RL, Müller-Schwarze D (eds) Chemical signals in vertebrates IV. Plenum Press,
1367 New York, pp 335–342
1368

1369 Reese ES (1989) Orientation behavior of butterflyfishes (family Chaetodontidae) on
1370 coral reefs: spatial learning of route specific landmarks and cognitive maps. *Devel Env*
1371 *Biol Fish* 9: 79-86
1372

1373 Rensch B (1957) Ästhetische Faktoren bei Farb- und Formbevorzugen von Affen.
1374 *Z Tierpsychol* 14: 71-99
1375

1376 Rensch B (1958) Die Wirksamkeit ästhetischer Faktoren bei Wirbeltieren. *Z*
1377 *Tierpsychol* 15: 447-461
1378

1379 Rodriguez F, Duran E, Vargas JP, Torres B, Salas, C (1994) Performance of goldfish
1380 trained in allocentric and egocentric maze procedures suggests the presence of a
1381 cognitive mapping system in fishes. *Anim Learn Behav* 22: 409-420
1382

1383 Rodríguez I, Gumbert A, Hempel de Ibarra N, Kunze J, Giurfa M (2004) Symmetry is
1384 in the eye of the beholder: innate preference for bilateral symmetry in flower-naïve
1385 bumblebees. *Naturwiss* 91:374–7
1386

1387 Rodriguez F, Broglio C, Durán E, Gómez Y, Salas C (2006) Neural mechanisms of
1388 learning in teleost fishes. In: Brown C, Laland K, Krause J (eds) *Fish cognition and*
1389 *behaviour*. Blackwell, Oxford, pp 243–277
1390

1391 Rodriguez-Moldes I (2009) A developmental approach to forebrain organization in
1392 elasmobranchs: New perspectives on the regionalization of the telecephalon. *Brain*
1393 *Behav Evol* 74: 20-29
1394

1395 Roitblatt HL, Tham W, Golub L (1982) Performance of *Betta splendens* in a radial arm
1396 maze. *Anim Learn Behav* 10: 108-114
1397

1398 Roth G, Grunwald S, Mühlenbrock-Lentner S (2004). Morphology and axonal
1399 projection pattern of neurons in the telencephalon of the fire-bellied toad *Bombina*
1400 *orientalis*. J Comp Neurol 478: 35-61.
1401

1402 Saigusa T, Tero A, Nakagaki T, Kuramoto Y (2008) Amoebae anticipate periodic
1403 events. Physical Review Letters 100 (1)
1404

1405 Salas C, Broglio C, Rodriguez F, Lopez JC, Portavella M, Torres B (1996a)
1406 Telencephalic ablation in goldfish impairs performance in a 'spatial constancy' problem
1407 but not in a cued one. Behav Brain Res 79: 193-200
1408

1409 Salas C, Rodriguez F, Vargas JP, Duran E, Torres B (1996b) Spatial learning and
1410 memory deficits after telencephalic ablation in goldfish trained in place and turn maze
1411 procedures. Behav Neurosci 110: 965-980
1412

1413 Salwiczek LH, Pretot L, Demarta L, Proctor D, Essler J, Pinto AL, Wismer S, Stoinski
1414 T, Brosnan SF, Bshary R (2012) Adult cleaner wrasse outperform capuchin monkeys,
1415 chimpanzees and orang-utans in a complex foraging task derived from cleaner – clint
1416 reef fish cooperation. PLOS 7: e49068
1417

1418 Sanders MJ, Wiltgen BJ, Fanselow MS (2003) The place of the hippocampus in fear
1419 conditioning. Eur J Pharmacol 463:217–223
1420

1421 Schluessel V, Bleckmann H. (2005) Spatial memory and orientation strategies in the
1422 elasmobranch *Potamotrygon motoro*. J Comp Physiol A 191: 695-706
1423

1424 Schluessel V, Bleckmann H (2012) Spatial learning and memory retention in the grey
1425 bamboo shark (*Chiloscyllium griseum*). Zool 115: 346-353
1426

1427 Schluessel V, Fricke G, Bleckmann H (2012) Visual discrimination and object
1428 categorization in the cichlid *Pseudotropheus* sp. Anim Cogn 15: 525-537
1429

1430 Schluessel V, Kraniotakes H, Bleckmann H (2014). Visual discrimination of rotated 3D
1431 objects in Malawi Cichlids (*Pseudotropheus* sp.): a first indication for form constancy
1432 in fishes. *Anim Cogn* 17: 559-371
1433

1434 Schluessel V, Beil O, Weber T, Bleckmann H (2014) Symmetry perception in sharks
1435 (*Chiloscyllium griseum*) and cichlids (*Pseudotropheus* sp.). *Anim Cogn* DOI
1436 10.1007/s10071-014-0751-2
1437

1438 Schlupp D, Ryan MJ (1997) Male sailfin mollies (*Poecilia latipinna*) copy the mate
1439 choice of other males. *Behav Ecol* 8: 104-107
1440

1441 Schuster S, Rossel S, Schmidtman, Jäger I, Piralla J (2004) Archer fish learn to
1442 compensate for complex optical distortions to determine the absolute size of their aerial
1443 prey. *Current Biol* 14: 1565-1568
1444

1445 Schuster S, Wöhl S, Griebisch M, Klostermeier I (2006) Animal cognition: how archer
1446 fish learn to down rapidly moving targets. *Current Biol* 16: 378–383
1447

1448 Schwarze S, Bleckmann H, Schluessel V (2013) Avoidance conditioning in bamboo
1449 sharks (*Chiloscyllium punctatum* and *C. griseum*): behavioural and neuroanatomical
1450 aspects. *J Comp Physiol A* 199:843–856
1451

1452 Segall MH, Campbell LT, Herskovits MJ (1966) The influence of culture on visual
1453 perception. Bobbs-Merrill, Indianapolis
1454

1455 Sherry DF, Vaccarino AL, Buckenham K, Herz RS (1989) The hippocampal complex
1456 of food-storing birds. *Brain Behav Evol* 34: 308–317
1457

1458 Sherry DF, Jacobs LF, Gaulin SJC (1992) Spatial memory and adaptive specialisation
1459 of the hippocampus. *Trends Neurosci* 15: 298–303
1460

1461 Shettleworth SJ (2010) Clever animals and killjoy explanations in comparative
1462 psychology. *Trends Cogn Sci* 14: 477-481
1463

1464 Shumway CA (2008) Habitat complexity, brain, and behavior. *Brain Behav Evol* 72:
1465 123-134
1466

1467 Siciliano AM, Kajiura SM, Long Jr. JH, Porter ME (2013) Are you positive? Electric
1468 dipole polarity discrimination in the yellow stingray *Urobatis jamaicensis*. *Biol Bull* 225:
1469 85-91
1470

1471 Siebeck UE, Litherland L, Wallis GM (2009) Shape learning and discrimination in reef
1472 fish. *J Exp Biol* 212: 2113-2119
1473

1474 Sims, DW; Southall, EJ; Richardson, AJ, Reid PC, Metcalfe, JD (2003) Seasonal
1475 movements and behaviour of basking sharks from archival tagging: no evidence of
1476 winter hibernation. *Mar Ecol Prog Ser* 248: 187-196
1477

1478 Smeets WJAJ, Nieuwenhuys R, Roberts BL (1983) The central nervous system of
1479 cartilaginous fishes. Structure and functional correlations. Springer, Berlin
1480

1481 Sovrano VA, Bisazza A, Vallortigara G (2002) Modularity and spatial reorientation in a
1482 simple mind: Encoding of geometric and nongeometric properties of a spatial
1483 environment by fish. *Cognition* 85: B51-B59
1484

1485 Sovrano VA, Bisazza A, Vallortigara G (2007) How fish do geometry in large and in
1486 small spaces. *Cognition* 10: 47-54
1487

1488 Sovrano VA, Bisazza A (2008) Recognition of partly occluded objects by fish. *Cognition*
1489 11: 161-166
1490

1491 Sovrano VA, Bisazza A (2009) Perception of subjective contours in fish. *Perception*
1492 38: 479-490
1493

1494 Spaet JLY, Kessel ST, Gruber SH (2010). Learned hook avoidance of lemon sharks
1495 (*Negaprion brevirostris*) based on electroreception and shock treatment. *Mar Biol Res*
1496 6: 399–407
1497

1498 Spinozzi, G (1996) Categorization in monkeys and chimpanzees. Behav Brain Res 74:
1499 17-24
1500

1501 Squire L (2004) Memory systems of the brain: A brief history and current perspective.
1502 Neurobiol Learn Mem 82:171–177
1503

1504 Srinivasan MV (2010) Honey bees as a model for vision, perception, and cognition.
1505 Ann Rev Entomol 55: 267 -284
1506 Striedter GF (1997) The telencephalon of tetrapods in
1507 evolution. Brain Behav Evol 49: 179-213

1508 Suboski MD, Bain S, Carty AE, McQuoid LM, Seelen MI, Seifert M (1990) Alarm
1509 reaction in acquisition and social transmission of simulated-predator recognition by
1510 zebra danio fish (*Brachydanio rerio*). J Comp Psychol 104: 101-112
1511

1512 Tarrant RM (1964) Rate of extinction of a conditional response in juvenile sockeye
1513 salmon. Trans Am Fish Soc 93:399–401
1514

1515 Tester A, Kato S (1963) Visual target discrimination in blacktip sharks (*Carcharhinus*
1516 *melanopterus*) and grey sharks (*C. menisorrah*). Pac Sci 20: 461–471
1517

1518 Teyke T (1989) Learning and remembering the environment in the blind cave fish
1519 *Anoptichthys jordani*. J Comp Physiol A 164:655–662
1520

1521 Thonhauser KE, Gutnick T, Byrne RA, Kral K, Burghardt GM, Kuba M (2013) Social
1522 learning in cartilaginous fish (stingrays *Potamotrygon falkneri*). Anim Cogn 16:927-932
1523

1524 Thünken T, Waitschyk N, Bakker TCM, Kullmann H (2009) Olfactory self-recognition
1525 in a cichlid fish. Anim Cogn 12: 717-724
1526

1527 Tigges M (1962) Muster- und Farbbevorzugung bei Fischen. Z Tierpsychol 20: 129-
1528 142
1529

1530 Vargas JP, Lopez JC, Salas C, Thinus-Blanc C (2004) Encoding of geometric and
1531 featural spatial information by goldfish (*Carassius auratus*). J Comp Psychol 2: 206-
1532 216
1533
1534 Vargas JP, López JC, Portavella M (2009) What are the functions of fish brain pallium?
1535 Brain Res Bull 79:436–40
1536
1537 Vargas JP, Quintero E, López JC (2011) Influence of distal and proximal cues in
1538 encoding geometric information. Anim Cogn 14: 351-358
1539
1540 von der Emde G (1999) Active electrolocation of objects in weakly electric fish. J Exp
1541 Biol 202: 1205-1215
1542
1543 von der Emde G, Behr K, Bouton B, Engelmann J, Fetz S, Folde C (2010) 3-
1544 Dimensional scene perception during active electrolocation in a weakly electric pulse
1545 fish. Frontiers Behav Neurosci 4: 26
1546
1547 Warburton K (1990) The use of local landmarks by foraging goldfish. Anim Behav 40:
1548 500-505
1549
1550 Warburton K (2003) Learning of foraging skills by fish. Fish Fisher 4: 203-215
1551
1552 Webster MM, Laland KN (2011) Reproductive state affects reliance on public
1553 information in sticklebacks. Proc Royal Soc B Biol Sci 278: 619-627
1554
1555 White KG (2001) Forgetting functions. Anim Learn Behav 29: 193-207
1556
1557 Wilkens LA, Hofmann MH, Wojtenek W (2002) The electric sense of the paddlefish: a
1558 passive system for the detection and capture of zooplankton prey. J Physiol 96: 363-
1559 377
1560
1561 Wood LS, Desjardins JK, Fernald R (2011) Effects of stress and motivation on
1562 performing in a spatial task. Neurobiol Learn Mem 95: 277-285
1563

1564 Wright T, Jackson R (1964) Instrumental conditioning of young sharks. *Copeia* 1964:
1565 409-12
1566

1567 Wullimann MF (1997) The central nervous system. In: Evans DH (ed) *Physiology of*
1568 *fishes*. CRC Press, Boca Raton, pp 245-282
1569

1570 Wullimann MF, Mueller T (2004) Teleostean and mammalian forebrains contrasted:
1571 Evidence from genes to behavior. *J Comp Neurol* 475: 143-62
1572

1573 Wunder W (1934) Gattenwahlversuche bei Stichling und Bitterling. *Deutsche*
1574 *Zoologische Gesellschaft* 36:152–158
1575

1576 Wyzisk K (2005) Experimente zur Formen- und Größenwahrnehmung beim Goldfisch
1577 (*Carassius auratus*) unter Verwendung von Scheinkonturen und Größentäuschungen.
1578 PhD Thesis, Johannes Gutenberg Universität Mainz
1579

1580 Wyzisk K, Neumeier C (2007) Perception of illusory surfaces and contours in goldfish.
1581 *Vis Neurosci* 24: 291-298
1582

1583 Yopak KE, Lisney TJ, Collin SP, Montgomery JC (2007) Variation in brain organization
1584 and cerebellar foliation in chondrichthyans: sharks and holocephalans. *Brain Behav*
1585 *Evol* 69: 280–300
1586

1587 Yopak KE, Frank LR (2009) Brain size and brain organization of the whale shark,
1588 *Rhincodon typus*, using magnetic resonance imaging. *Brain Behav Evol* 74:121–142
1589

1590 Yopak KE (2012a) Neuroecology in cartilaginous fishes: the functional implications of
1591 brain scaling. *J Fish Biol* 80:1968–2023
1592

1593 Yopak KE (2012b) The nervous system of cartilaginous fishes. *Brain Behav Evol*
1594 80:77–79
1595

1596 Yue S, Moccia RD, Duncan IJH (2004) Investigating fear in domestic rainbow trout,
1597 (*Oncorhynchus mykiss*), using an avoidance learning task. Appl Anim Behav Sci
1598 87:343–354
1599
1600 Zerbolio DJ, Royalty JL (1983) Matching and oddity conditional discrimination in the
1601 goldfish as avoidance responses: evidence for conceptual avoidance learning. Anim
1602 Learn Behav 11:341–348
1603
1604
1605

1606 Figure legends

1607

1608 Fig. 1a Fuss et al (2014a): Transfer results for the egocentrically trained group. While
1609 none of the three sharks showed any significant preference for any one arm during T1,
1610 all sharks of this group highly significantly preferred the learned turn procedure in T2
1611 and T3. The correct arm is marked by an asterisk. The correct swimming pathways are
1612 indicated by arrows. 1b: Transfer results for the ego-allocentrically trained group. Two
1613 of the three sharks did not show any significant preference for any one arm during T1,
1614 all sharks of this group highly significantly preferred the learned turn procedure in T2
1615 and T3. The correct arm is marked by an asterisk (in case of egocentric orientation) or
1616 a circle (in case of allocentric orientation). The correct swimming pathways are
1617 indicated by arrows (reproduced from Fuss et al. 2014a, J Comp Physiol).

1618

1619 Fig. 2 Fuss et al (2014b): Results of the transfer trials of the allocentrically trained
1620 group (T1 – T7). Partial elimination of visual cues did not influence sharks' performance
1621 during T1-T4 transfer trials. When eliminating all visual cues (T5), sharks were no
1622 longer able to find the correct exit. When altering the position of one SC by 90° within
1623 the setup, sharks did not significantly prefer one exit (reproduced from Fuss et al.
1624 2014b, J Comp Physiol).

1625

1626 Fig. 3 Schluessel et al (2014): Example of stimulus pairs shown during the regular trials
1627 in the categorisation experiments. The symmetrical symbol on the left was always the
1628 positive stimulus. Both symbols were projected simultaneously and fish had to chose
1629 the positive one to obtain a food reward (reproduced from Schluessel et al. 2014, Anim
1630 Cogn).

1631

1632 Fig. 4 Fuss et al (2014d): Stimuli presented to each group during regular training and
1633 transfer test trials in Experiments 1a and 1b. The positive, rewarded stimulus is
1634 indicated by a checkmark. In Group 1 an empty square was the positive, rewarded
1635 stimulus, in Group 2 it was an empty triangle. During the transfer tests of Experiment
1636 1a, sharks were 'expected' to choose the correct Kanizsa figure. During Experiment
1637 3b, Group 1 was trained to recognize an empty square over an empty triangle, whereas
1638 Group 2 was trained vice versa. During the transfer tests, sharks were expected to

1639 choose the Kanizsa figure resembling the stimulus they had been trained on
 1640 (reproduced from Fuss et al. 2014d, Front Neural Circuits).

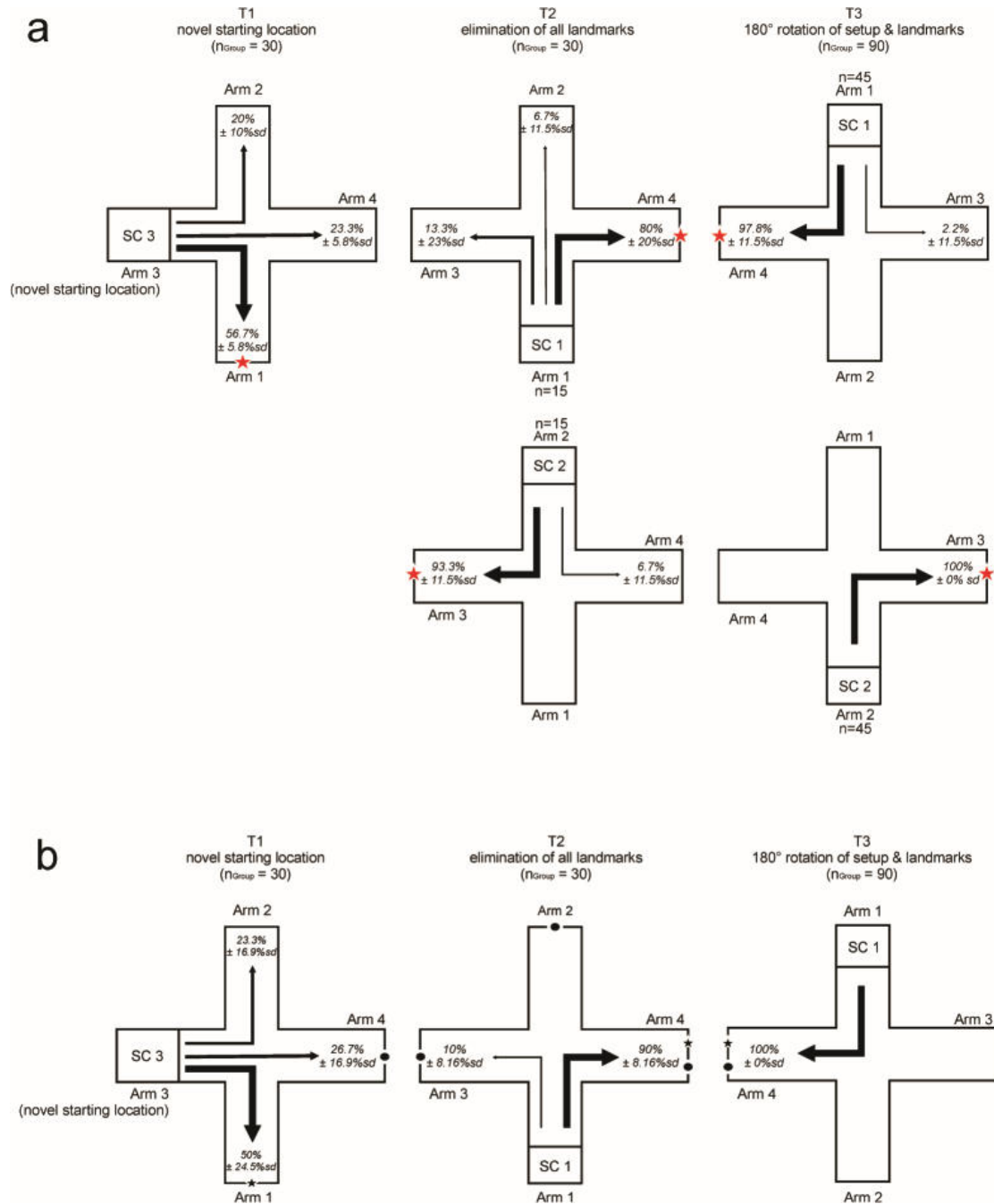
1641

1642 Figures

1643

1644 Figure 1

1645



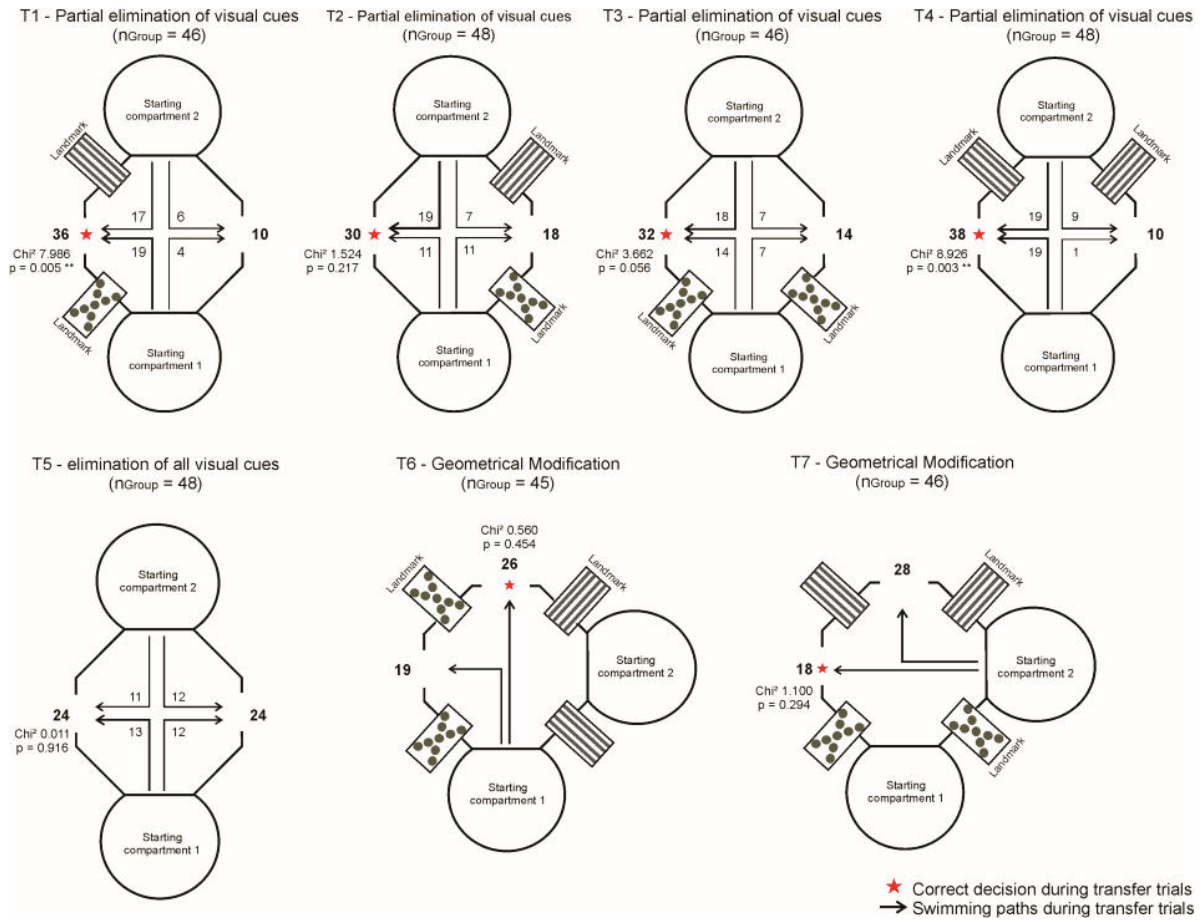
1646

1647

1648

1649 Figure 2

1650



1651

1652

1653

1654

1655

1656

1657

1658

1659

1660

1661

1662

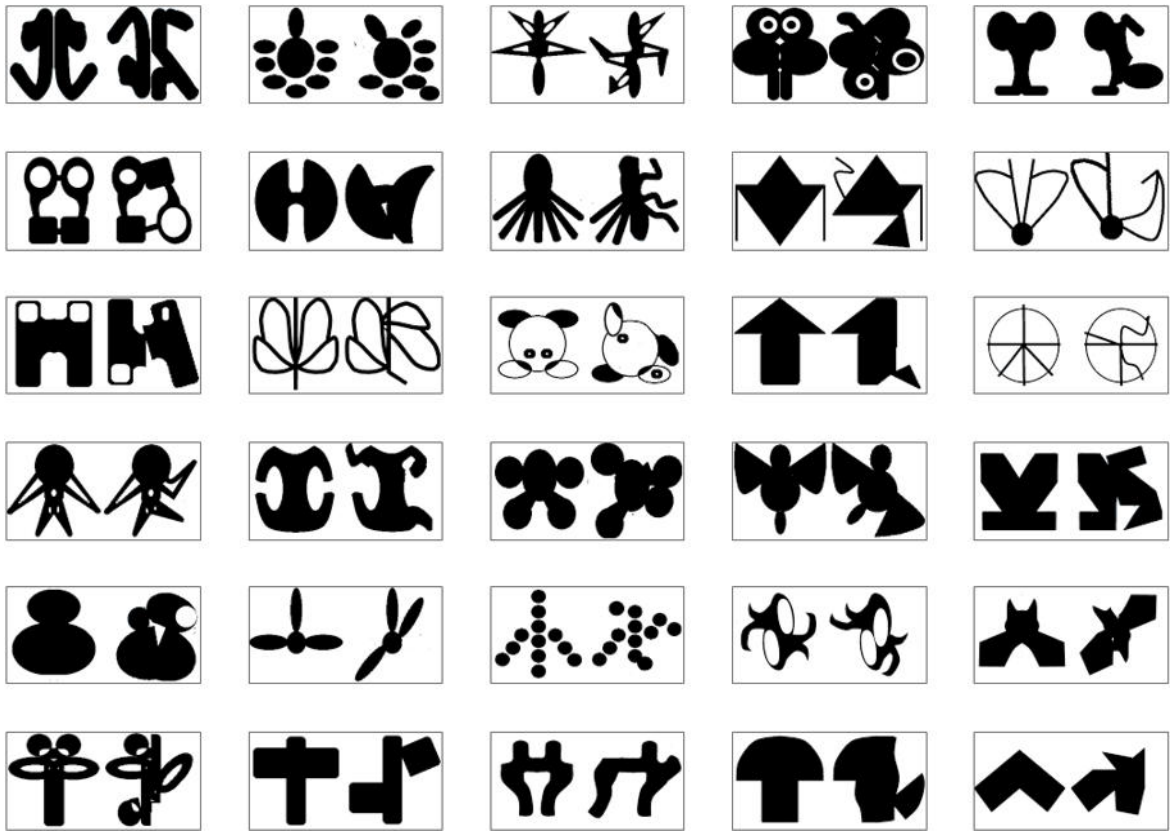
1663

1664

1665

1666

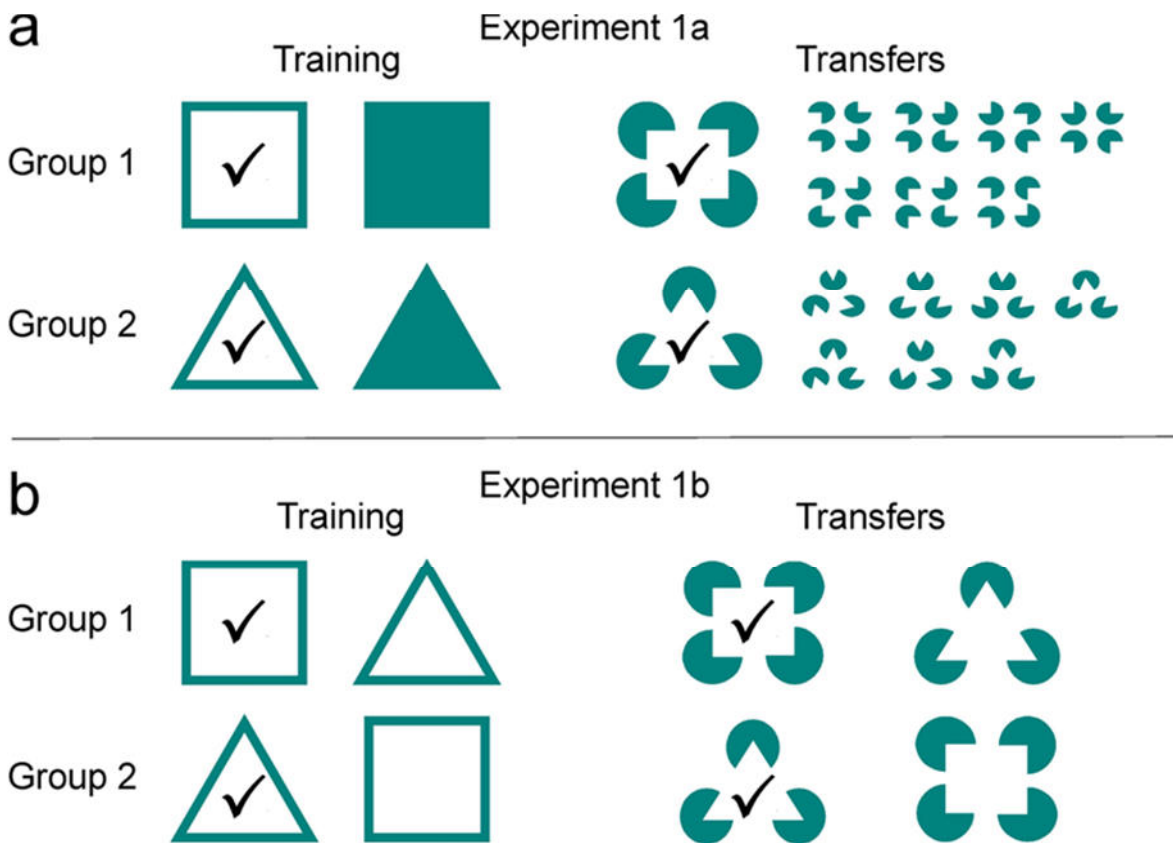
1667 Figure 3



1668

1669

1670 Figure 4



1671