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7 **Video playback demonstrates episodic personality in the gloomy octopus**

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## SUMMARY

Coleoid cephalopods, including octopuses, cuttlefish and squid, rely mainly on visual signals when interacting with conspecifics, predators, and prey. Presenting visual stimuli, such as models, photographs, mirrors, and live conspecifics, can thus provide insight into cephalopod behaviour. These methods, however, have limitations- mirrors and live animals lack experimental control, whereas models and photographs sacrifice motion-based information. Video playback addresses these issues by presenting controlled, moving, and realistic stimuli, but, to date, video playback has not been used successfully with any cephalopod. Here, we developed a video playback technique for the gloomy octopus (*Octopus tetricus*) that incorporated recent advances in video technology. We then used this technique to test for personality, which we defined as behavioural differences between individuals that are consistent over time and across ecologically important contexts. We captured wild octopuses and tested them on three separate days over a 10-day period. On each test day, subjects were presented with videos of a food item, novel object, and a conspecific. These represented a foraging, novel, and threatening context, respectively. A fourth video without a moving stimulus controlled for the playback monitor itself and potential artifacts associated with video playback. Experimental stimuli evoked unambiguous and biologically appropriate responses from the subjects. Furthermore, individuals' responses to the three experimental contexts were highly correlated within a given test day. However, within a given context, individuals behaved inconsistently across the three test days. The reordering of ranks suggests that rather than fulfilling the criteria for personality, gloomy octopus show temporal discontinuities, and hence display episodic personality.

Key words: *Octopus tetricus*, cephalopod, video playback, visual signal

## INTRODUCTION

47  
48 Visual signals and cues are critical in many species for tasks such as predator recognition  
49 (Blumstein et al., 2000; Tinbergen, 1951), predator avoidance (Otte, 1974), species  
50 recognition (Bradbury and Vehrencamp, 1998), and social communication (Ord et al., 2002).  
51 Presenting controlled visual stimuli is therefore important for determining the function of  
52 visual signals and cues in these species. Traditionally, visual stimuli have included models or  
53 inanimate objects (Hemmi and Zeil, 2003), pictures (Dawkins, 1996), live animals (Herzog  
54 and Burghardt, 1974), conspecifics (Evans and Marler, 1991), or mirrors (Povinelli et al.,  
55 1997). Each of these stimuli has limitations- mirrors and live animals offer little experimental  
56 control, whereas models and photographs sacrifice potentially salient motion-based  
57 information.

58 Video playback provides a unique method for presenting moving visual stimuli that are  
59 both controlled and realistic. Video stimuli can also be manipulated easily with video editing  
60 software and are unaffected by the behaviour of the subject being tested. But video  
61 playback is not without its challenges. For example, video was designed for the human  
62 visual system, so differences in the visual systems of other animals means they may  
63 perceive video differently than humans. Spatial and temporal resolution, the lack of a third  
64 dimension, and the representation of colour and brightness may all affect how video stimuli  
65 are perceived by animals (for reviews see D'Eath, 1998; Fleishman et al., 1998; Zeil, 2000).  
66 Nevertheless, by addressing many of these issues, video playback has been used successfully  
67 with a variety of species, including arachnids, crustaceans, fish, reptiles, amphibians, birds  
68 and primates (Ord et al., 2002).

69 Coleoid cephalopods, including octopuses, cuttlefish, and squid, rely heavily on visual  
70 signals and cues when interacting with conspecifics, predators, and prey (Hanlon and  
71 Messenger, 1996). Their skin can display brilliant colours and striking patterns that are used  
72 for signaling in a variety of contexts, including social communication, defence and prey  
73 capture (Langridge, 2009; Moynihan and Rodaniche, 1982; Warren et al., 1974). They also  
74 have large eyes with high visual acuity, focal lengths similar to fish (Hanlon and Messenger,  
75 1996), and flicker fusion rates of up to 60 Hz (Hamasaki, 1968). They cannot discriminate  
76 between different hues, but they can see polarized light (Hanlon and Messenger, 1996). By  
77 presenting them with visual stimuli such as inanimate objects (Sinn and Moltschaniwskyj,  
78 2005), live animals (Mather and Anderson, 1993), and mirrors (Adamo and Hanlon, 1996),

79 previous research has gained considerable insight into cephalopod visual behaviour. No  
80 study, however, has elicited biologically appropriate responses from cephalopods using  
81 video playback.

82 In the present study, we developed a successful video playback technique for the gloomy  
83 octopus, *Octopus tetricus* (Gould, 1852), and then used this technique to test for the  
84 presence of personality, which is also known as behavioural syndromes, temperament and  
85 individuality. We defined ‘personality’ as a suite of intercorrelated personality traits (Kurvers  
86 et al., 2009) and ‘personality traits’ as interindividual differences in behaviour that are  
87 consistent over time and context (Biro and Stamps, 2008; Kurvers et al., 2009). ‘Consistent’  
88 in this sense means that interindividual differences in the expression of a trait are  
89 maintained, but that the absolute level of expression can be variable (Réale et al., 2007).  
90 Such phenotypic variation, both between and within individuals, may result from intrinsic  
91 factors, such as experience, hormone levels, and physiological state (e.g., Frost et al., 2006;  
92 Koolhaas et al., 1999). In dumpling squid (*Euprymna tasmanica*), for example, individual  
93 differences can be attributed to sex, body size, genetic composition, and sexual maturity  
94 (Sinn and Moltschaniwskyj, 2005; Sinn et al., 2006; Sinn et al., 2007). Of course, extrinsic  
95 factors, such as environmental conditions, food availability, predation risk, and the social  
96 environment, can also affect the expression of personality traits (e.g., Biro and Stamps,  
97 2008; Brown et al., 2007; McGuire et al., 1994).

98 We used video playback to present focal individuals with three types of experimental  
99 stimuli representing three different ecologically important contexts. We presented each  
100 stimulus to each subject on each of three days, and we recorded several response variables.  
101 Our objectives were to test (1) whether video playback evokes biologically appropriate  
102 responses from the gloomy octopus and (2) whether subjects respond consistently over  
103 time and across multiple contexts.

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## MATERIALS AND METHODS

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### Subjects

108 Thirty one gloomy octopuses (*O. tetricus*) were caught by hand in bays within Sydney  
109 Harbour, Sydney, Australia (33° 50' S, 151° 22' E) between May and September 2008. They  
110 were transported to the Sydney Institute of Marine Science, Chowder Bay, Sydney. Before

111 transferring them to holding tanks, they were weighed using a 1000 g Pesola spring scale  
112 (accuracy:  $\pm 10$  g), or, for those exceeding 1000 g, a 3000 g Scientech electronic balance  
113 (accuracy:  $\pm 0.01$  g). Sex could not be determined reliably, as the majority of subjects were  
114 small and would not have had a fully developed hectocotylus.

115 At the Sydney Institute of Marine Science, each octopus was housed in a separate  
116 opaque plastic tank (60 x 36 x 27 cm, l x w x h) that received a constant flow (approx. 1 L per  
117 min) of filtered seawater from Chowder Bay. The floor of each tank was covered with  
118 pebbles, rocks, and pieces of pipe, and a terracotta pot was provided as shelter. The  
119 aquarium facility was maintained on a natural daylight cycle via skylights and fluorescent  
120 lights (approximately 10 h light per day during May, June, July; 11 h light per day during  
121 August; 13 h per day during Sept). Octopuses were fed thawed, frozen prawn or squid every  
122 second day in the evening. Octopuses exceeding 400 g received two to three prawns or half  
123 of a squid, whereas those weighing less than 400 g received one prawn or one quarter of a  
124 squid. On test days, feeding occurred in their home tank at least 30 min after testing was  
125 complete. Octopuses were kept for a minimum of ten days for experimentation, after which  
126 they were released at sites not closer than 2 km to any collection site. The gloomy octopus  
127 is a sedentary species and individuals occupy permanent lairs (Norman and Reid, 2000). It is  
128 therefore unlikely that released individuals were subsequently recaptured.

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### **Video Stimuli**

131 The video stimulus types included footage of a novel object (jar), a food item (crab,  
132 *Leptograpsus variegatus*), a conspecific, and a control (water-filled aquarium). For each  
133 stimulus type, three different exemplars (i.e. 12 stimuli in total) were created to reduce  
134 pseudoreplication and ensure that behavioural responses to the stimuli reflected the  
135 stimulus type and not some idiosyncrasy of a particular exemplar. Consistent with previous  
136 work, the novel object was used to test the subject's boldness and/or exploratory behaviour  
137 (Réale et al., 2007). The crab is a preferred food item of the gloomy octopus and was  
138 therefore used to simulate a foraging context. As octopuses are asocial, solitary, largely  
139 intolerant, and in some species aggressive toward conspecifics (Hanlon and Messenger,  
140 1996), the conspecific footage was used to simulate a threatening, aggressive encounter.  
141 Video of a water-filled aquarium served as a control, which accounted for the presence of  
142 an illuminated monitor and for potential motion artifacts associated with video playback.

143 Stimuli were video recorded in a glass aquarium (122 x 35 x 51 cm) filled with seawater.  
144 The aquarium was lit by four 60 W incandescent globes and by natural light from overhead  
145 skylights. The rear of the aquarium was covered with a white cloth, which formed the  
146 background of each clip (see Table S1 in supplementary material). The crab, however, was  
147 difficult to view while positioned flat on the aquarium bottom. We therefore placed a  
148 moveable plastic floor under the crab and tilted it slightly towards the camera  
149 (approximately 15° above horizontal) to provide a more complete view of the stimulus (see  
150 Table S1 in supplementary material). Footage was shot with a Sony HDR-HC7 Handicam  
151 (format: HDV1080i50; shutter speed: 1/100 s) and was recorded digitally to the hard drive of  
152 an Apple computer (Mac Mini 2.0 GHz Intel Core Duo) using Quicktime Pro software (v. 7,  
153 Apple Inc., Cupertino, CA, USA). The camera's optical zoom was set so that a section of the  
154 middle of the aquarium, including the floor, occupied the entire field of view.

155 For each of the 12 exemplars, footage was edited using Final Cut Pro software (v. 6,  
156 Apple Inc.) to make a three-min sequence in which the stimulus made several alternating  
157 passes across the aquarium (see stimuli descriptions in Table S1 in supplementary material).  
158 Each stimulus moved off screen at the end of each pass and entered again from the side it  
159 exited to simulate a realistic movement. The 12 three-min clips were then exported for  
160 playback as QuickTime video files (format: DVCPRO720p50).

161 Finally, we measured the size, brightness, and movement of the nine experimental video  
162 stimuli (i.e. 3 crab, 3 novel objects, 3 conspecifics) so that these properties, independent of  
163 stimulus type, could be related to the subjects' behavioural responses. Size was measured  
164 on the monitor used for playback. The size of each conspecific video stimulus was described  
165 by the lateral length from the eyes to the end of the mantle. The size of each novel object  
166 stimulus was described by its maximum width, while the size of each crab video stimulus  
167 was described by the maximum width of its carapace. Octopuses cannot discriminate  
168 between different hues (Hanlon and Messenger, 1996), so we measured brightness instead  
169 of colour. This was measured using Colour Picker Pro software (v. 3.1.0, Critical Matter Inc.,  
170 Salt Lake City, UT, USA) on the computer broadcasting the stimuli. Specifically, we measured  
171 brightness at 10 random locations on each novel object stimulus, 10 random locations on  
172 the mantle of each conspecific stimulus, and 10 random locations on the carapace of each  
173 crab stimulus. The average of each set of 10 brightness measurements was then used to  
174 approximate the brightness value of each of the nine video stimuli. Note that the contrast

175 between the stimulus and its background was not measured because the background  
176 brightness was held constant across all stimulus videos. Finally, we measured movement by  
177 counting the number of alternating passes that each stimulus made across the playback  
178 monitor. Supplementary table 1 provides a complete description of the stimuli created.

179

### 180 **Playback Apparatus**

181 During tests, subjects were placed in the same glass aquarium that was used to record  
182 video stimuli. It was filled with filtered seawater and was visually isolated from the  
183 surroundings by white cloth and black screens (see Fig. 1). To facilitate scoring, the  
184 aquarium was placed on top of a Cartesian coordinate grid that divided the floor into 32  
185 equal squares (see Fig 1). Stimuli were played using Final Cut Pro software (v. 5, Apple Inc.)  
186 on a Macintosh computer (Mac Mini 2.0 GHz Intel Core Duo), and were broadcast to  
187 subjects on a 43 cm BenQ LCD monitor (50 Hz refresh rate; 1280 x 1024 lines of resolution,  
188 0.264 mm pixel pitch) that was placed firmly against one end of the aquarium (Fig 1). This  
189 approach is similar to that used by Rosenthal et al. (1996), in which sword-tail fish  
190 responded realistically and appropriately to video stimuli played on a screen abutting the  
191 subject's tank. A Sony HDR-HC7 Handicam placed directly above the aquarium provided a  
192 live view of the aquarium to a remote laptop computer (Macbook 2.0 GHz Intel Core Duo),  
193 which recorded the subjects' responses using Quicktime Pro software (v. 7, Apple Inc.;  
194 format: HDV1080i50).

195

### 196 **Test Procedure**

197 Each octopus was tested on three separate days: the day after capture, four days later and  
198 four days later again. All testing occurred in the late afternoon so it that it finished within  
199 one hour of sunset (gloomy octopuses are crepuscular and nocturnal; Norman and Reid,  
200 2000).

201 Immediately prior to testing, the subject was caught with a hand net from it's home tank  
202 and transferred to one of two water-filled plastic boxes that was fitted with a door on one  
203 side (8 x 8 x 19 cm with 8 cm diameter door for octopuses under 1 kg; 22 x 22 x 22 cm with  
204 10 cm diameter door for subjects exceeding 1 kg). The box was then transferred into the  
205 *start arena* of the test aquarium (end of aquarium opposite monitor, Fig 1), and, after 3 min  
206 of habituation, the door of the box was opened remotely. Octopuses were given a maximum

207 of 15 min to emerge from the box into the surrounding test aquarium. If they did not  
208 emerge during this time, the box was slowly lifted out of the water until the subject exited  
209 through the door (the subject was never held out of water for more than 5 s). Immediately  
210 following emergence, the box was replaced with a terracotta pot that provided the subject  
211 with refuge during subsequent stimulus presentations.

212 Following emergence from the box, the subject was given 3 min to habituate to the test  
213 aquarium. One exemplar (selected at random and without replacement) of each of the four  
214 stimulus types was then shown in a randomly determined sequence. The first of the four  
215 stimuli was presented when the subject entered the *start arena*. Each subsequent stimulus  
216 was then presented after a minimum of 3 min following the completion of the previous  
217 stimulus, at a time when the subject was again within the *start arena*. If, for any stimulus  
218 presentation, the subject did not move to the *start arena* after 10 min, the stimulus was  
219 presented regardless of the subject's position. If a subject had inked or produced any  
220 noticeable secretions whilst being tested, the water in the test aquarium was replaced  
221 before the next subject was tested.

222 Throughout the trial, except when broadcasting a video stimulus, the monitor displayed a  
223 still image of the control stimulus (i.e., a water-filled aquarium; see Table S1 in  
224 supplementary material). The transition to each stimulus clip was then softened using a  
225 4-frame cross-dissolve transition to ensure that stimulus presentations did not begin or end  
226 with a sudden change in brightness on the monitor. To prevent interference from the  
227 observer, video playbacks were controlled remotely using Remote Desktop software (v. 3,  
228 Apple Inc.) running on the same laptop computer that was used to record the subject's  
229 response. Subjects were returned to their home tank immediately after testing using a net  
230 and water-filled bucket.

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### **Data Scoring**

233 Test footage was scored on a 30" monitor using Final Cut Pro software (v. 6, Apple Inc.) on a  
234 Macintosh Computer. For each of the three test days, five response variables were  
235 measured during each of the four video presentations. These included latency, movement,  
236 number of stimulus touches, brightness change (range between lightest and darkest colour),  
237 and chromatic/textural change. Scoring was done blind with respect to subject identity and



238 test day for all variables. In addition, brightness change and chromatic/textural change were  
239 scored blind with respect to stimulus type.

240 Latency was recorded as the time taken for the subject's eye to cross the first gridline  
241 (parallel to the playback monitor) between the subject and the monitor after a stimulus  
242 commenced. Reference to the eye was used in all measurements, as it is the most central,  
243 recognisable point on octopuses. Movement was measured by recording the subject's  
244 position relative to the Cartesian coordinate grid at 20 s intervals throughout the 3 min  
245 stimulus presentation. The distances moved between each 20 s interval were calculated  
246 using the Pythagorean theorem and were then summed to provide an estimate of the  
247 subject's total movement for that 3 min period. The number of times that the subject  
248 touched the end of the aquarium displaying the stimulus was also noted.

249 The brightness level corresponding to the majority of the body's surface area (excluding  
250 arms) was scored according to a seven point ordinal scale. The lightest skin colour observed  
251 across all subjects was assigned a score of one and the darkest colour a score of seven  
252 (scores two through six were distributed evenly between these two values). Brightness  
253 scores were assigned by comparing the brightness of the subject to that of seven still images  
254 that corresponded to the seven brightness values. The same images were used to score all  
255 trials, thereby ensuring that all measurements were made relative to the same standards.  
256 Chromatic/textural pattern, as defined by Hanlon and Messenger (1996) was scored  
257 according to a four point ordinal scale. A score of one indicated that textural patterns (i.e.  
258 erect papillae) and/or colour patterns (i.e. chromatic arrangement) were absent from the  
259 entire body, whereas a score of four indicated that a texture and/or colour pattern was  
260 evident over the entire body. Scores of two and three indicated a colour pattern and/or  
261 textural pattern on one and two thirds of the body, respectively. Brightness level and  
262 chromatic/textural pattern scores were recorded 10 s prior to each stimulus presentation.  
263 Maximum scores observed throughout each stimulus presentation were also noted. For  
264 each stimulus presentation, the pre-stimulus scores were subtracted from the maximum  
265 scores to obtain difference scores that reflected the subject's maximum change in  
266 brightness level and chromatic/textural pattern in response to that particular stimulus.

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268

### **Data Analysis**

269 To control for putative differences in individuals' daily motivational states (e.g. hunger),  
270 the latency, movement, number of stimulus touches, brightness change, and  
271 chromatic/textural pattern change were corrected using a baseline measure of each. To  
272 achieve this, each response measure exhibited during the control stimulus on a particular  
273 day was subtracted from that recorded for each experimental stimulus on that same test  
274 day. The behaviour expressed during the control is an ideal baseline measure, as the control  
275 stimulus is identical to the other stimulus types (i.e. video of a water-filled aquarium),  
276 except that it lacks a moving object. Principal components analysis (orthogonal rotation  
277 method: varimax) was then conducted on the five baseline-corrected response variables to  
278 reduce them to a smaller number of orthogonal factors (Table 1). The resulting factor scores  
279 were used in all data analyses.

280 General linear mixed models with repeated fixed factors were used to analyse the  
281 population-level responses and determine if subjects responded differently to the three  
282 different stimulus types (i.e. conspecific, crab, novel object). Test day and stimulus type  
283 were included as repeated fixed factors, and subject weight as a covariate. Separate models  
284 were run on each of the orthogonal factors derived from the principal components analysis.  
285 Where an overall model was significant, post hoc pairwise comparisons were used to  
286 identify statistically significant differences. Overall type I error was controlled using the  
287 sequential Bonferroni method (Holm, 1979; Rice, 1989).

288 Pearson correlations were conducted on each principal component to test whether  
289 individuals responded consistently across the three experimental contexts on each day (i.e.  
290 conspecific, crab, and novel object), and across the three test days within each experimental  
291 context. A measure of repeatability ( $R$ ), as described by Lessells and Boag (1987), was also  
292 provided for each correlation matrix to describe the overall consistency of individuals'  
293 behaviour.

294 Finally, we used multiple linear regression to test for a possible relationship between  
295 stimulus characteristics, independent of stimulus type, and subjects' behavioural responses.  
296 Independent variables included stimulus size, the number of passes that the stimulus made  
297 across the screen, and stimulus brightness. A separate analysis was conducted for each of  
298 the nine experimental trials (i.e. excluding the three control trials) and for each of the  
299 derived principal components.

300 For all analyses, data complied with the parametric assumptions of normality and  
301 homogeneity of variance, as determined by Kolmogorov-Smirnov tests (all  $p > 0.098$ ) and  
302 inspection of histograms. All tests were conducted in SPSS 16.0 (SPSS Inc., Chicago, IL, USA),  
303 were two-tailed, and had an  $\alpha$  level of 0.05.

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## RESULTS

307 The principal components analysis generated two principal components that together  
308 accounted for 68.10% of the variance contained in the original five response variables.  
309 Movement, latency and the number of stimulus touches were highly intercorrelated, as all  
310 of them loaded heavily onto the first principal component (Table 1). Movement and the  
311 number of stimulus touches correlated positively with each other and negatively with  
312 latency. Chromatic/textural pattern change loaded heavily onto the second principal  
313 component, and brightness change loaded approximately equally onto both principal  
314 components.

315 At the population level, there was a significant difference in subjects' responses to the  
316 three different stimulus types (general linear mixed model, PC1:  $F_{2,170} = 11.583$ ,  $P < 0.0001$ ,  
317 Fig. 2; PC2:  $F_{2,165} = 5.661$ ,  $P = 0.004$ , Fig. 3). During the food item presentation, subjects  
318 approached significantly faster, moved greater distances, and touched the stimulus more  
319 often, as compared to the presentations of the conspecific and novel object (Fig. 2, Mov. 1  
320 in supplementary material). Approaches to the conspecific stimulus were the slowest and  
321 there was less movement and fewer stimulus touches than in response to the food item and  
322 novel object stimuli (Fig. 2, Mov. 2 in supplementary material). Subjects also exhibited a  
323 chromatic/texture change over more of their body during presentation of the food item  
324 stimulus than during presentation of either a novel object or conspecific (Fig. 3). Finally, we  
325 detected no interaction between the stimulus type and test day for PC1 (general linear  
326 mixed model,  $F_{4,123} = 0.179$ ,  $P = 0.949$ ) or PC2 ( $F_{4,131} = 0.154$ ,  $P = 0.961$ ), suggesting that  
327 subjects habituated to the four stimulus types at approximately the same rate throughout  
328 the experiment.

329 On any given day, subjects' responses to video presentations of the food item,  
330 conspecific, and novel object were highly intercorrelated (all  $R > 0.36$ , Tables 2, 3, 4). PC1  
331 and PC2 were both significantly and positively correlated among the three contexts within

332 each of the three test days (Tables 2, 3, 4). Therefore, individual octopuses behaved  
333 consistently with respect to their activity and body pattern within a given test day.

334 In marked contrast, gloomy octopus behaviours were inconsistent from one day to the  
335 next in response to any particular stimulus type (all  $R < 0.07$ ). The principal component  
336 scores were not correlated over the three test days for any stimulus type (Table 5). As an  
337 example of this inconsistency, subject 1 responded to the conspecific stimulus on test day  
338 one by immediately approaching it, touching it repeatedly with its arms extended, erecting  
339 its papillae, and flashing dark colouration. In contrast, on test day 2 that same subject  
340 avoided the conspecific stimulus, remained motionless behind the pot, and only erected its  
341 papillae on a small section of skin.

342 Of the 18 multiple linear regression analyses conducted (2 response variables; 9 tests  
343 involving experimental stimuli), there were only two significant linear relationships between  
344 subjects' responses and the properties of the stimuli shown to them. Stimulus size and  
345 stimulus brightness together explained a significant amount of the variation in both PC1  
346 (multiple linear regression analysis,  $F_{3,25} = 8.12$ ,  $P = 0.001$ ,  $R^2_{adj} = 0.703$ ; size:  $t = -2.342$ ,  $p =$   
347  $0.027$ ; colour (brightness):  $t = -2.091$ ,  $p = 0.047$ ) and PC2 ( $F_{3,25} = 13.21$ ,  $p < 0.02$ ,  $R^2_{adj} = 0.369$ ;  
348 size:  $t = -2.116$ ,  $p = 0.044$ ) during the fifth video stimulus presentation. No other significant  
349 linear relationships existed between PC1 or PC2 and the size, colour, and movement of the  
350 stimuli (multiple linear regressions, all  $P > 0.063$ ).

351

352

## 353 DISCUSSION

### 354 Video responses

355 Gloomy octopuses reacted differently to the three different video stimuli (Figs 2, 3). Their  
356 responses to the stimuli were also biologically appropriate. For example, subjects rapidly  
357 approached the crab stimulus- often using jet propulsion (Mov. 1 in supplementary  
358 material)- and repeatedly touched the stimulus while simultaneously displaying dark  
359 colouration and pronounced body patterns. This sequence of behaviours is qualitatively  
360 similar to the crab attack sequence described for free-living octopuses by Maldonado (1964)  
361 and Packard (1963). In response to the conspecific stimulus, most subjects reduced their  
362 activity and avoided the stimulus, often cowering at the far end of the tank or seeking  
363 refuge behind or inside the terracotta pot (Fig. 2, Mov. 2 in supplementary material). In the

364 wild, octopuses are solitary animals that actively avoid conspecifics (Byrne et al., 2004;  
365 Hanlon and Messenger, 1996). Aggressive encounters with conspecifics are also costly and  
366 can result in severe damage, such as loss of arms (e.g., Aronson, 1986). Our subjects'  
367 seemingly adaptive responses to simulated conspecifics were therefore consistent with  
368 responses to live conspecifics in the wild. This study therefore provides the first  
369 demonstration that video playback can evoke stimulus-specific and biologically appropriate  
370 responses from a cephalopod.

371 Prior to conducting this experiment, there were no published accounts in which video  
372 playback had been presented to cephalopods. We therefore optimised every parameter  
373 that has been shown to be important in previous studies with other taxa to increase the  
374 probability that subjects would respond appropriately to video stimuli (for reviews see  
375 D'Eath, 1998; Fleishman and Endler, 2000; Zeil, 2000). This included using high-definition  
376 stimuli broadcast at 50 frames per second. As cephalopods have excellent spatial acuity  
377 (Hanlon and Messenger, 1996) and high flicker fusion rates of approximately 60 Hz  
378 (Hamasaki, 1968), these parameters were probably critical for creating realistic stimuli. In  
379 addition, we broadcast stimuli on an LCD monitor. Unlike conventional CRT monitors, the  
380 pixels on LCD monitors do not flash on and off between screen refreshes, but, rather,  
381 update themselves without turning off, which prevents known problems associated with  
382 refresh-induced flicker (D'Eath, 1998). However, LCD monitors use polarizing filters that  
383 cause each pixel to be polarized in a different way. Although octopuses use polarized light  
384 patterns when interacting with predators, prey, and conspecifics (Shashar and Cronin, 1996;  
385 Shashar et al., 2000), potential polarization artifacts associated with our LCD monitor did  
386 not prevent subjects from responding appropriately to video stimuli. Nevertheless,  
387 polarization is an important factor to consider in future video playback studies with  
388 cephalopods. Finally, we avoided artifacts associated with interlaced video (e.g., ghosting or  
389 jagged and distorted images) by converting our stimuli to progressive scan video before  
390 presenting them to subjects.

391

392

### **Personality**

393 Individuals behaved consistently across the three experimental contexts (conspecific,  
394 foraging, novel object) on any given test day, which was reflected by strong correlation  
395 coefficients and high measures of repeatability (Tables 2-4). For example, an individual that

396 aggressively attacked the crab stimulus on day one (i.e., quick approach, high levels of  
397 movement, touched the stimulus many times) was also relatively aggressive towards the  
398 conspecific and the novel object on day one. The gloomy octopus therefore satisfies part of  
399 our definition of personality, which is that interindividual differences in behaviour are  
400 consistent across multiple contexts (Biro and Stamps, 2008; Kurvers et al., 2009).

401 In marked contrast, none of the personality traits were repeatable over time (Table 5).  
402 An individual that was bold, aggressive and exploratory on day one was just as likely to have  
403 been shy, submissive, and stationary in the same context on day two. Although personality  
404 traits can change with time or experience, the relative ranks of individuals should remain  
405 the same (Réale et al., 2007). As subjects did not meet this requirement, they violated a key  
406 requirement of personality, which is that personality traits are consistent over time. This  
407 suggests that the gloomy octopus does not have personality, but, rather, that it has an  
408 'episodic' personality.

409 The negative results obtained from the repeatability analysis were not simply a result of  
410 insufficient statistical power. Indeed, power analysis revealed that a sample of only 24  
411 individuals would be necessary to detect a moderate effect (correlation coefficient of 0.7)  
412 with a power of 0.8 (two-way test,  $\alpha = 0.05$ ). Furthermore, our comparisons of behaviour  
413 across contexts within the same day involved precisely the same sample of subjects, yet all  
414 of the 18 correlations in that analysis were statistically significant (Tables 2-4). In  
415 comparison, none of the 18 correlations in the repeatability analysis were statistically  
416 significant (Table 5), suggesting that octopus behaviours were genuinely inconsistent over  
417 multiple test days.

418 Low repeatability also cannot be attributed readily to our experimental design. For  
419 example, a possible explanation for episodic personality is that subjects' motivational states  
420 varied from one day to the next, perhaps as a function of varying levels of hunger. This  
421 seems unlikely, however, because behaviours expressed in each experimental context on  
422 any given day were corrected for baseline behaviour observed in the control treatment on  
423 that same day. Finally, low repeatability can occur when the environment in which the  
424 repeated measures are obtained is highly variable (Réale et al., 2007). Again, this seems  
425 unlikely, as our test apparatus and experimental stimuli were stringently controlled.

426 Some previous studies of personality have shown that individuals' behaviours are  
427 correlated only in certain contexts and only over certain periods of times. For example,

428 Mather and Anderson (1993) showed that octopus' behaviour in response to alerting,  
429 threatening and feeding tests could be reduced into principal components that represented  
430 broader dimensions of personality, but, as in our study, these were not consistent over the  
431 two week test period (Mather and Anderson, 1993). Similarly, adult dumpling squid  
432 displayed context-specific personality traits during feeding and threat tests, but these traits  
433 were repeatable only in the threat tests (Sinn and Moltschaniwskyj, 2005). Furthermore,  
434 over the entire lifetime of the dumpling squid, personality traits were consistent both  
435 before and after sexual maturation, before sexual maturation being before 9 weeks of age  
436 and after sexual maturation being after 16 weeks of age (Sinn et al., 2007). But, during  
437 sexual maturation, from 9 to 12 weeks of age, the degree of consistency varied significantly  
438 among different personality types (Sinn et al., 2007). Finally, in stickleback (*Gasterosteus*  
439 *aculeatus*), personality type also decouples over time. Similar to the gloomy octopus, the  
440 stickleback may be aggressive, bold and active at one point in time, but, later in life, the  
441 same individual may express a completely different personality (Bell and Stamps, 2004).  
442 Thus, some species show stability of personality over time, whereas others show no stability  
443 over time, or stability only in certain life phases.

444 There are a variety of mechanisms that could underlie the short-term behavioural  
445 correlations observed in our study. For example, octopuses have an advanced neural  
446 system, which is reflected by their capacity for associative learning and their long-term  
447 memory in both visual and tactile tasks (Hanlon and Messenger, 1996; Hochner, 2008). This  
448 large neuronal capacity may afford octopuses considerable behavioural flexibility that  
449 allows them to change their behaviour adaptively over time. Alternatively, short-term  
450 behavioural correlations may result from a physiological process, such as the release of  
451 hormones that affect multiple behaviours (Ketterson and Nolan, 1999). Activational effects  
452 of hormones are generally short-term, as they are more easily altered by modifications of  
453 hormonal pathways (Elekovich and Robinson, 2000). Consequently, behavioural correlations  
454 that have an endocrine basis can also have a short duration (Sih et al., 2004). For example, a  
455 chemosensory cue - most likely a pheromone - elicits strong aggressive behaviour in longfin  
456 shore squid (*Loligo pealeii*) (Buresch et al., 2003).

457 Gloomy octopuses live in highly heterogeneous environments that fluctuate over both  
458 spatial and temporal scales (Anderson, 1997). According to the adaptive plasticity  
459 hypothesis, these conditions may select for behavioural flexibility, as individuals could then

460 optimise their behaviour in a variety of typical environmental conditions (Van Buskirk,  
461 2002). For example, behaving shyly might be an individual's optimal response when it is  
462 being threatened by a predator, whereas behaving boldly might be that same individual's  
463 optimal response in a foraging context a short time later. However, complete behavioural  
464 plasticity can be costly because of the energetic costs associated with the requisite sensory  
465 and regulatory mechanisms (reviewed in DeWitt et al., 1998). A species' degree of  
466 behavioural flexibility may hence reflect a tradeoff between the associated costs and  
467 benefits, which, in turn, may be affected by the volatility of that species' environmental  
468 conditions. For the gloomy octopus, it may be advantageous to forgo plasticity over short  
469 periods of time in which environmental conditions are relatively constant. In the lab, this  
470 period of time might correspond to the brief duration of our trials on any particular test day,  
471 which might explain why behaviours were correlated across contexts but not across test  
472 days.

473

474

### **Conclusion**

475 Our study provides the first evidence that video playback can elicit biologically  
476 appropriate responses from a cephalopod. Given the importance and the complexity of  
477 visual signaling in this group, we believe that video playback will be a valuable tool for  
478 studying a wide range of cephalopod behaviours, including visual communication, learning,  
479 and social and reproductive behaviour. In addition, we showed that subjects' responses to  
480 one functionally important class of stimuli predicted their responses to other important  
481 classes of stimuli on the same test day. However, subjects' responses during our relatively  
482 short test period were inconsistent from one day to the next, which suggests that the  
483 gloomy octopus has an episodic personality.

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485

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607 limitations of video playback techniques. *Acta. Ethol.* **3**, 39–48.

608

609 **Table 1.** Factor loadings for the principle components derived from a principal components  
610 analysis conducted on five response variables. Orthogonal rotation method: varimax.

Variable	PC1	PC2
Movement	0.897	0.010
Latency	-0.866	-0.068
Stimulus touches	0.754	-0.097
Brightness Change	0.477	0.411
Chromatic/Texture Change	-0.105	0.928
% of variance explained	47.35	20.75

611

612 **Table 2** Pearson correlations for test day one for PC1 (values below and left of diagonal) and  
613 PC2 (values above and right of diagonal).

Stimulus type	Food Item	Novel Object	Conspecific
Food Item		0.511**	0.544**
Novel Object	0.415*		0.476**
Conspecific	0.577**	0.522**	

\*p<0.05, \*\*p<0.001 (two-tailed)  
Repeatability measure for PC1 across the three contexts on day one,  $R=0.60$   
Repeatability measure for PC2 across the three contexts on day one,  $R=0.49$

614

615

616 **Table 3.** Pearson correlations for test day two for PC1 (values below and left of diagonal)  
 617 and PC2 (values above and right of diagonal).

Stimulus type	Food Item	Novel Object	Conspecific
Food Item		0.496**	0.408*
Novel Object	0.600**		0.577**
Conspecific	0.606**	0.612**	

\*p<0.05, \*\*p<0.001 (two-tailed)  
 Repeatability measure for PC1 across the three contexts on day two, R=0.49  
 Repeatability measure for PC2 across the three contexts on day two, R=0.43

618

619

620 **Table 4.** Pearson correlations for test day three for PC1 (values below and left of diagonal)  
621 and PC2 (values above and right of diagonal).

Stimulus type	Food Item	Novel Object	Conspecific
Food Item		0.628**	0.508**
Novel Object	0.483**		0.707**
Conspecific	0.495**	0.653**	

\* $p < 0.05$ , \*\* $p < 0.001$  (two-tailed)  
Repeatability measure for PC1 across the three contexts on day three,  $R = 0.42$   
Repeatability measure for PC2 across the three contexts on day three,  $R = 0.36$

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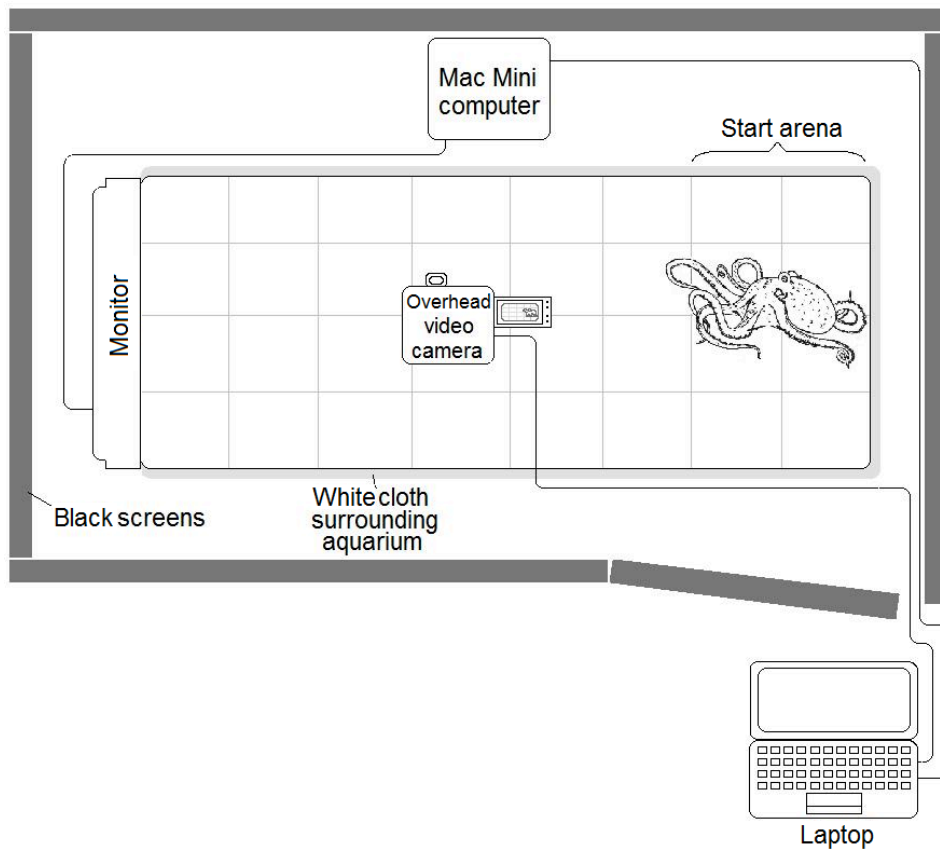
624 **Table 5.** Pearson correlations and repeatability values (*R*) between each test day for PC1 and  
 625 PC2 within each stimulus type.

	Between Days	Food Item	Novel Object	Conspecific
PC1	1 and 2	-0.127	0.088	0.034
	1 and 3	-0.205	-0.094	-0.127
	2 and 3	0.231	-0.209	-0.194
	<i>R</i> =	0.000	0.044	0.000
PC2	1 and 2	-0.162	0.037	-0.016
	1 and 3	-0.008	0.062	-0.226
	2 and 3	0.210	-0.074	-0.021
	<i>R</i> =	0.044	0.012	0.074

\**p*<0.05, \*\**p*<0.001 (two-tailed)

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 627

628 Fig 1.



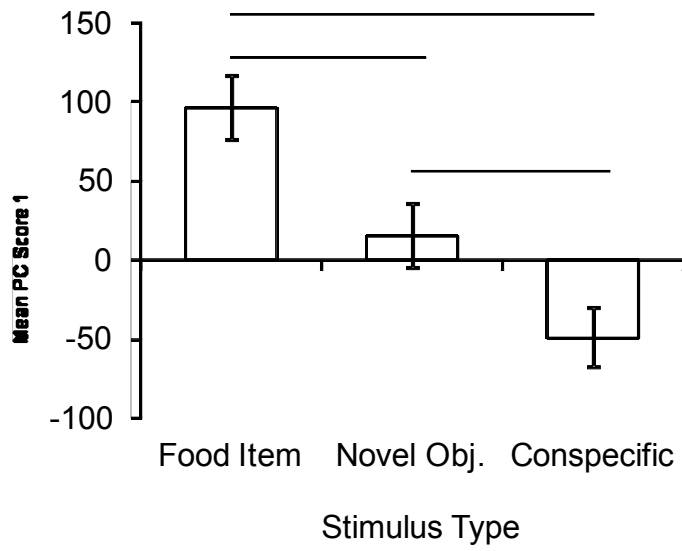
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631 **Fig. 1.** Overhead schematic of test apparatus. Diagram not to scale.

632

633 Fig 2.



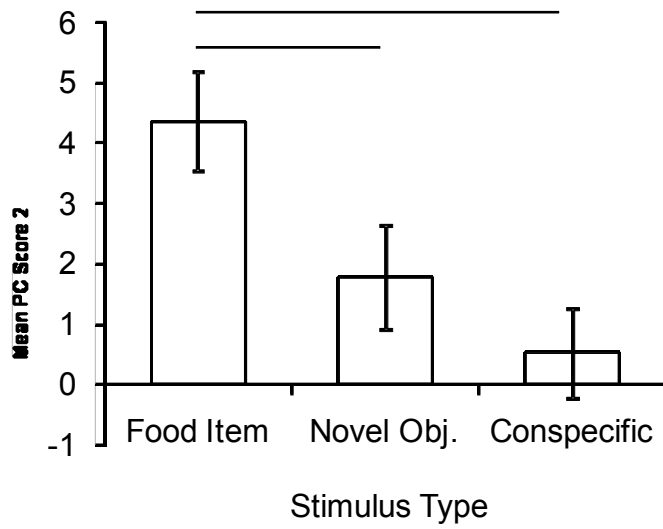
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636 **Fig. 2.** Mean PC1 responses ( $\pm$  s.e.m.) of 31 *O. tetricus* to three types of experimental  
637 stimuli, averaged across the three test days. Bars indicate a significant difference between  
638 treatments (overall type I error controlled using the sequential Bonferroni method).

639

640 Fig 3.



641

642

643 **Fig. 3.** Mean PC2 responses ( $\pm$  s.e.m.) of 31 *O. tetricus* to three types of experimental  
644 stimuli, averaged across the three test days. Bars indicate a significant difference between  
645 treatments (overall type I error controlled using the sequential Bonferroni method).

646





647

**SUPPLEMENTARY MATERIAL**

648

649 **Table S1.** Description of the four stimulus types presented to subjects during the video

650 playback experiment. Values are averages of the three exemplars.

Stimulus Type	Number of passes across screen	Size on screen	Photo example of one exemplar
Food Item	15	3.5 cm carapace width	
Novel Object	23	5.5cm x 8.9cm high	
Conspecific	12	5.5cm mantle length	
Control	-	-	

651

652

653 **Movie S1.** Video footage of a gloomy octopus responding to a food item stimulus, as viewed  
654 from directly above the test aquarium. The window superimposed in the bottom left corner  
655 shows the time-locked stimulus video that was presented to the subject.

656

657 **Movie S2.** Video footage of a gloomy octopus responding to a conspecific stimulus, as  
658 viewed from directly above the test aquarium. The window superimposed in the bottom left  
659 corner shows the time-locked stimulus video that was presented to the subject.

660