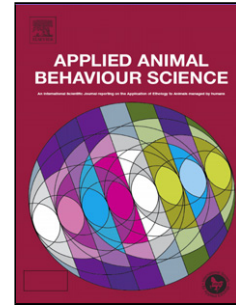


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1 Individual differences in visual and olfactory cue preference and use by cats (*Felis*
2 *catus*)

3

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15 Research highlights

- 16 • Eight cats were trained in a T-maze using a two-alternative forced choice procedure
- 17 • Cats could use either an olfactory or visual cue to locate a food reward
- 18 • Cues were then put in conflict to determine which was preferred for the task
- 19 • Most cats used the visual cue to learn the location of the food
- 20 • Preferences were stable, repeatable and rapidly learned

21

22

23

23 **Abstract**

24

25 Animals are constantly presented with stimuli through different sensory challenges,
26 which may sometimes contain contradictory information and so they must decide which
27 is more salient in a given situation. Both vision and olfaction are extensively utilised by
28 the domestic cat (*Felis catus*) in a variety of biological contexts, but which modality
29 tends to take priority when the two channels contain information of similar potential
30 value is unknown, as is the tendency for different individuals to use different cues in
31 relation to the same situation. Such individual difference may have important clinical
32 implications as it may help to explain why animals living within the same house may
33 respond differently to the same environment. For example a change in the olfactory
34 features of the environment may be stressful to an individual who has a bias towards
35 using this sensory modality, but have no significant impact on individuals who rely
36 more on visual cues for orientation. Eight cats were trained in a T-maze using a two-
37 alternative forced choice procedure. The positive and negative stimuli presented both
38 visual and olfactory information. Thus, there were two cues that the cats could use in
39 order to make the discrimination. After reaching criterion for their training stimuli the
40 six successful cats were presented with a feature mismatch test in which the positive
41 visual stimuli were combined with the negative olfactory stimuli and vice versa. This
42 investigated which cues were of greater salience to them. Four out of six cats showed a
43 significant preference ($P = 0.022- 0.006$) for the visual cue, but one individual showed a
44 consistent preference for using the olfactory cue ($P = 0.019$). To investigate whether the
45 cats using visual cues had learned anything about the olfactory stimulus, four were
46 given an additional test in which they were presented with the olfactory stimulus alone.
47 Three out of four cats successfully made this discrimination, ($P = 0.006-0.003$,
48 unsuccessful cat $P = 0.076$). This demonstrated that the cats had the potential to use
49 olfactory cues in the absence of visual ones. These results highlight the importance of

50 considering sensory preferences as an individual trait, which may vary substantially
51 from population level effects.

52

53 **Keywords**

54 Cat, Intermodal discrimination, Learning, Multisensory, Olfaction, Vision

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55 **1. Introduction**

56 An animal's ability to discriminate between environmental stimuli and prioritise
57 attention to certain features is considered critical to its survival. Cues for discrimination
58 can be considered as any environmental stimulus that an animal is able to use and learn
59 about (Saleh et al., 2007). As the natural environment is typically multi-sensory (e.g.
60 Rowe, 2005), it is likely that cues can exist in any, or all, sensory modalities. This
61 results in a vast amount of potential information arriving within the perceptual systems.
62 It is inconceivable that an animal can process, learn about and respond appropriately to
63 all this information (Huber and Wilkinson 2011). Different cues or modalities are likely
64 to be more salient than others when making certain types of discrimination, but those
65 used by a given animal may be influenced by individual experience, within the
66 constraints of the species' fundamental perceptual capacities (Phillmore, 2008). Thus,
67 understanding the use of different sensory modalities during equivalent learning, tasks
68 provides critical insight into the translation of ability to performance in real-world
69 environments.

70 Currently, very little is known about the use of different modalities in cue
71 learning in non-human animals. There is, however, some interesting work on the use of
72 different cues within a modality. The majority of this work has been done with pigeons
73 (*Columba livia*). Pigeons have a highly developed visual system (Cook, 2001) and are
74 widely used in studies of visual discrimination. Intramodal sensory discrimination
75 experiments have investigated the mechanisms which allow them to visually
76 discriminate different cues (e.g. stimulus colour, shape, orientation Lea and Harrison
77 1978; geometric dimensions Lea et al., 1993; and geometric shapes Wills et al., 2009).
78 These experiments have used artificial stimuli which allow the precise determination of
79 the dimensions which control discriminatory behaviour (e.g. Lea and Harrison, 1978;
80 Lea et al., 1993; Wills et al., 2009). Generally, when pigeons are presented with
81 multidimensional stimuli, colour predominates (e.g. Lazareva et al., 2005). However

82 they are able to use pattern and shape information but rarely, if ever, use all the stimulus
83 dimensions that are available to them in a discrimination task (Lea and Wills, 2008;
84 Wills et al., 2009). In a similar type of study cats presented with compound stimuli
85 contrasting size, shape and brightness were found to respond most to the brightness cue
86 (Hara and Warren, 1961). However, these stimuli were trained separately and combined
87 only during the tests.

88 Investigation of learning across modalities generally examines different learning
89 rates for different stimulus modalities separately (see Slotnick, 2001 for a review) and
90 rarely compares learning novel discriminations using multisensory stimuli. Though
91 interesting, this type of stimulus separation does not allow the investigation of
92 allocation of attention to complex stimuli that are more similar to those which an animal
93 experiences in its natural environment. Some work has investigated differences in
94 discrimination abilities in sniffer dogs using a compound stimulus approach in a
95 tracking task (Gazit and Terkel, 2003, Wells and Hepper, 2003). Results suggest that
96 they use odour rather than vision to solve the task. However, these findings are
97 necessarily biased by the use of animals trained to make odour discriminations and thus
98 reveal little information about learning across modalities.

99 It is also important to investigate individual differences in this process as this
100 may have clinical significance. Problem behaviour, such as urine spraying in indoor
101 cats, may be expressed by one individual within the home but not another, even though
102 all individuals are exposed to the same environment. While these differences can be
103 explained in terms of differences in temperament such as trait anxiety (Dehasse 1997),
104 the extent to which these changes arise because of differences in sensory bias in creating
105 the animal's umwelt and thus the perception of environmental stressors appears to have
106 been overlooked. Examining whether there are individual differences in sensory choice
107 when learning across modalities in the same task, provides a first step to explore the
108 potential for this to occur.

109 The domestic cat (*Felis catus*), like the dog, is macrosmatic (Reznik 1990), but
110 it also has excellent vision and a large binocular field (Pettigrew 1986). In this species,
111 different sensory modalities appear to predominate at different stages of development.
112 Kittens are born blind and so, during the immediate postnatal period, depend largely on
113 olfactory cues for teat-search and attachment behaviour (Raihani et al., 2009) and nest
114 directional cues (Rosenblatt, 1972). From three weeks, vision is thought to take a more
115 central role and visual cues appear to be used to locate and learn social skills from
116 interactions with the mother (Bateson, 2000) and heterospecifics (Crowell-Davis, 2003).
117 To our knowledge, there are no studies that have investigated the use of multisensory
118 stimuli in controlled settings in the species, nor the consistency of individual differences
119 in sensory preferences in decision making. Therefore, the present study investigated
120 which cue from an intermodal visual and olfactory compound stimulus is used by
121 individual cats when learning to discriminate novel stimuli. We tested the null
122 hypotheses that there was no preference for visual over olfactory cues or the converse,
123 at either population or individual level.

124

125 **2. Materials and methods**

126 **2.1 Subjects**

127 Eight cats (six males, two females, all neutered, mean age 3.3 years range 8 months to 7
128 years) took part in the study, six were shelter cats taken in from owners who could no
129 longer keep them and housed at the Cat Welfare Centre at The University of Lincoln
130 with a view to rehoming into families, and two were family owned.

131

132 **2.2 Stimulus materials**

133 **2.2.1. Visual cues**

134 Six visual cues were used: blue, brown, green, purple, red and yellow (spectral
135 reflectance data provided in Fig. 1). These are within the cats' capacity to discriminate

136 on the basis of colour as well as brightness (Brown et al., 1973; Loop and Bruce, 1978;,
137 Kezeli et al., 1987). Each visual stimulus was printed onto white paper in the shape of a
138 10cm square with 2cm white border and laminated. This stimulus area was chosen to
139 ensure that it was large enough for a cat to perform a colour discrimination (Loop et al.,
140 1978).

141

142 Insert Figure 1 around here

143

144 **2.2.2 Olfactory cues**

145 Six single compounds were used as olfactory stimuli (details in Table 1), which have all
146 been used in previous animal and human studies (e.g. honeybees, Laska and Galizia,
147 2001; squirrel monkeys, Laska et al., 1999; humans, Laska and Teubner, 1999). Single
148 compounds were used rather than complex blends of different odorous molecules
149 because this allows greater control over the stimulus being presented. All odorants were
150 single molecule compounds (Table 1) obtained from Sigma-Aldrich Co LLC
151 (Gillingham Dorset UK).

152 The concentrations of the stock solutions were chosen as they are perceived to have the
153 same intensity to humans relative to a reference odour (8.7 g/L isoamyl acetate in
154 diethyl phthalate), in accordance with Laska et al. (1999). Thus, the stock solutions
155 were matched in perceived intensity at the concentrations stated. They were diluted with
156 99% diethyl phthalate as this solvent is nominally odourless (Laska et al. 1999). Once
157 diluted, the solutions were transferred to individual 25mL clear glass bottles with rubber
158 screw caps and individually labelled. Individual odours were presented by pipetting
159 0.75 mL of each odorant onto a 3cm² square filter paper (Fisherbrand) immediately
160 before a trial began. Fresh odour was applied to a new filter paper for each trial.

161

162 Insert Table 1 here

163

164 **2.2.3 Training stimuli**

165 Training stimuli consisted of pairs of compound stimuli containing both olfactory and
166 visual elements. One compound stimulus would be initially associated with food (S+)
167 and the other with no food (S-). When the cat had learned how to find food reliably, the
168 individual sensory elements of the compound stimuli were separated and used to make
169 new compound stimuli (using the S+ odour with S- visual element to make one new
170 compound stimulus and the S- odour with the S+ visual element to make the other) to
171 create a “Cue conflict test” (see below). To create these compound stimuli, an odour-
172 treated piece of filter paper was placed centrally at the top of one of the coloured
173 squares.

174 The combination of six potential visual and six olfactory elements resulted in 36
175 possible compound stimuli. These compound stimuli were pseudo-randomly paired,
176 with the constraint that no specific stimulus was present twice within a pair (i.e. each
177 pair of compound stimuli consisted of two different olfactory and two different visual
178 elements), to make 18 sets. One compound stimulus within each set was randomly
179 designated as a positive (S+) and the other compound stimulus a negative (S-) cue
180 according to whether it was associated with food or not.

181 For each cat, one set was designated for use to assess the initial preference (set 1) and a
182 different set (set 2) designated to test the robustness of the modality preference.

183 Insert Table 2 here

184

185 **2.3 Apparatus**

186 The experimental apparatus consisted of a free standing T-maze constructed of medium-
187 density fibreboard. The maze consisted of a central runway (width 31 cm x length 92
188 cm x height 51cm), at the end of which was the decision point with a left and right arm
189 (width 31 cm x length 61 cm x height 51 cm). Three white cat flap frames (i.e. plastic
190 cat flap products with the flap part removed to create a portal 34cm height x 28cm

191 width), divided the arms and central runway from the decision point (Fig. 2). Training
192 stimuli were suspended in front of the portals leading into each arm. The inside of the
193 maze was painted with a neutral grey gloss because this colour was not present among
194 the visual elements of the sets used, while gloss paint allowed the apparatus to be wiped
195 down easily with disinfectant between trials. The apparatus was covered by a thin wire
196 mesh. A detachable cat carrier was positioned at the base of the central runway alley
197 and acted as a start box. The apparatus was set up in a test room separate from the cats'
198 normal living area.

199

200 Insert Figure 2 here

201 The experimenter wore disposable gloves during cleaning and stimulus preparation, in
202 order to prevent contamination. To record the cats' behaviour a video camera (Canon
203 Legria HF R506) was situated at the two-choice point, recording at 50 frames/s.

204

205 **2.4 Procedure**

206 The experiment was run over a period of 4 months between February and June 2012.

207

208 **2.4.1. Pre-training 1: Entering cat carrier.**

209 All cats were trained to readily enter their own cat carrier before being introduced to the
210 T-maze, i.e. each cat had its own carrier so there was no chance of odour transfer
211 between subjects.

212

213 **2.4.2. T-maze habituation.**

214 Each cat was habituated to the apparatus without test stimuli present. To encourage
215 exploration, preferred food was scattered throughout the maze. Each habituation session
216 lasted 15 min or until all the food had been consumed. The habituation criterion was
217 considered met when the cat consumed all the food in two consecutive sessions.

218

219 **2.4.3. Pretraining 2: Approaching a stimulus in the maze.**

220 During this phase the S+ from the first stimulus set (set 1) was presented at the decision
221 point once on each side. When the cat approached the decision point and looked in the
222 direction of S+ a food reward was introduced into the arm behind the stimulus by the
223 experimenter. After consuming the food, the cat was removed from the T-maze. Two
224 pre-training trials were conducted per cat. A cat was not pre-trained with the S-, since
225 the goal was to emphasise the salience of the S+.

226

227

228 **2.4.4. General Procedure.**

229 All cats were trained and tested on one stimulus set and then this procedure was
230 repeated on a second stimulus set (see Table 2 for full details). The cats were tested
231 individually in the maze. A two-alternative forced choice procedure was used. A trial
232 started with the cat being placed into the start box. The box was then opened. The trial
233 time commenced when the cat left the start box, after which it had a maximum of 5 min
234 to make a choice; all cats made a choice within this time period. If the cat did not leave
235 the start box within 2 min of the door opening, the door was shut and food was rattled
236 once, before the door was reopened and the trial was rerun. A choice was counted once
237 the cat put its head through either portal. The apparatus was cleaned with disinfectant
238 wipes before the onset of each trial, to minimise the risk of an influence from any scent
239 marks deposited during the trial (Laska and Galizia, 2001) and fresh odour applied to
240 new filter paper.

241

242 **2.4.5. Discrimination learning**

243 Discrimination training consisted of 10 trials a session, with a minimum 2-min inter-
244 trial interval. A maximum of three training sessions occurred in any given day, 12
245 sessions (120 trials) were undertaken in total. More than one cat was trained on any
246 given day.

247 On each training trial the cat was presented with two stimuli, an S+ and an S- in front of
248 the portal leading to the arms of the T-maze. The position of the S+ was
249 pseudorandomised within a session; it was presented five times on the left and five
250 times on the right, with a maximum of three consecutive trials on the same side. If the
251 cat chose the S+, the trial was counted as correct, and a reward was delivered to the end
252 of the correct arm. If the cat chose the S-, the trial was counted as incorrect and the cat
253 was removed from the apparatus without receiving a reward. To reach criterion a cat
254 had to make 21/30 correct choices in the final 30 trials of the 12 sessions. Two cats
255 (Lily and Leon) were withdrawn at the end of training as they did not reach criterion.

256

257 **2.4.6. Cue conflict test.**

258 This test was undertaken the day after the discrimination learning threshold had been
259 reached. The aim of this test was to determine which element of the compound stimulus
260 (olfactory or visual) the cats used when making the discrimination. Thus, for the test
261 trials, the cues were presented in conflict with each other. The S+ visual cue was
262 presented in combination with the S- odour cue and vice versa. Three test trials were
263 presented per session; they were intermixed with 10 training trials resulting in a total of
264 13 trials per test session. The cats received a total of 12 test trials divided evenly among
265 four sessions. This procedure was repeated with a different stimulus set, so each cat was
266 exposed to two stimulus sets in total. Test trials were identical to training trials except

267 that no differential reinforcement was provided and the animals were removed from the
268 apparatus as soon as a choice was made.

269

270 **2.4.7. Odour only test.**

271 Four of the cats undertook a further set of tests. This test was identical to the cue
272 conflict test except that no visual information was presented. The odour cue of each
273 trained stimulus compound was presented on white visual stimuli measuring 12cm².

274

275 **2.5 Statistical analysis**

276 For the six cats reaching the training criterion, summary statistics were calculated and
277 the training data evaluated for normality using the Kolmogorov-Smirnov normality test
278 ($P=0.200$). To establish whether cats had learned to make a significant discrimination,
279 performance within each stimulus set was assessed initially by comparing the number of
280 correct trials in sessions 1 and 12 against chance performance (5/10 trials correct) using
281 a one-sample t -test. To determine whether learning was occurring across sessions for a
282 given stimulus set, the difference in performance between sessions 1 and 12 within a
283 session was compared using a paired t -test.

284 Binomial tests were conducted on the test data to determine individual preferences. The
285 p -values obtained from a binomial test for each cat over the two stimulus sets were
286 combined using the averaging method of Vovk (2012) to yield a single p -value for each
287 cat.

288

289

290 **3. Results**

291 There was no evidence of learning within session 1 of the first stimulus set with
292 performance not significantly different to chance i.e. 5/10 correct trials ($t = 0.24$, $df = 5$,
293 $P = 0.822$; Fig. 3). However, by session 12 performance was significantly better than
294 chance ($t = 25.00$, $df = 5$, $P < 0.001$; Fig. 3) and a significant preference for the S+ was

295 maintained when animals were exposed to stimulus set 2, with performance in both
296 sessions 1 and 12 significantly better than chance ($t = 4.00$, $df = 5$, $P = 0.010$; $t = 10.38$,
297 $df = 5$, $P < 0.001$, respectively). There was a significant difference in performance across
298 the sessions for stimulus set 1 (session 1 vs 12: $t = -6.30$, $df = 5$, $P = 0.001$), but no
299 significant difference across the sessions for stimulus set 2 ($t = -1.70$, $df = 5$, $P = 0.137$).
300

301

302 Insert Figure 3 here

303

304 Using cumulative binomial probability distributions, the cue conflict test revealed that
305 all but one of the animals had a significant preference for using one of the stimulus
306 dimensions (Table 3). All, except cat 3 used the visual stimulus significantly more than
307 the odour; cat 3 did the opposite.

308

309 Insert Table 3 here

310

311 The probability tests on the odour alone test revealed that, despite preferentially using
312 the visual cue when the cues were put in conflict, the cats had still learned about the
313 odour cue (Table 4).

314

315 Insert Table 4 here

316

317 **4. Discussion**

318 These results indicate that cats can learn to use a compound (visual-olfactory) stimulus
319 cue to make a discrimination, and when the cues are presented in conflict most cats, in
320 this test, used the visual information rather than the odour information. Learning was
321 clearly evident when the first stimulus set was used, but no significant difference was

322 observed when using the second stimulus set. A probable reason why no significant
323 difference across sessions was seen the second time is that the cats were already primed
324 to attend to the compound stimulus as a predictor of food and maintained their stimulus
325 modality preference from the previous set. Thus they would rapidly learn within the
326 first session how to use the S+ cue to locate the food (Fig. 3).

327 The small sample size, does not allow us to infer a general preference for cats to use
328 visual over olfactory stimuli when learning the location of food, or indeed for cats in
329 general within this specific experimental context. Nonetheless, this work does highlight
330 significant individual differences which might arise from either genetic or experiential
331 differences in the sample used. Early experience modulates the organisation and
332 function of the visual and olfactory sensory systems, and subject age in this study
333 ranged from 8 months to 7 years. Therefore, it is possible that age may have influenced
334 the discriminability and cue choice of individuals, but a larger sample size would be
335 required to determine this.

336 Interestingly, one animal chose significantly on the basis of odour information. Those
337 animals that did preferentially use the visual cue had learned about the odour cue and
338 when this was presented alone they were able to discriminate the positive from the
339 negative odour at a high level.

340 It is important to note that the observed use of visual stimuli over odour stimuli
341 may be context specific. The ability, or tendency, of an animal to use one type of
342 stimulus as a cue in one setting (stimulus predominance) does not mean that they
343 always do so. This could be because in other contexts other cues are available, or,
344 because a cue may relate to specific signals with a particular biological function.
345 Plasticity of cue use is likely to be highly adaptive. For example it has been found that
346 female three-spined sticklebacks (*Gasterosteus aculeatus*) rely on visual signals for
347 mate choice in clear water but predominantly use olfactory cues in turbid water
348 (Heuschele et al., 2009).

349 The role of species specific tendencies over individual experience cannot be
350 pulled apart within our current data. The subjects in this study were a population of pet
351 cats with diverse experience and extensive individuality. Such diversity reduces the
352 power to detect group level effects, but has the advantage of highlighting individual
353 differences that might exist in real world situations. Thus, it is worth noting that while
354 the cats generally used the visual stimuli rather than the odour stimuli when the
355 information was put into conflict, one individual used odour. Given that the cats were
356 pet animals, it might be speculated that they have developed a visual bias like pet dogs
357 compared to their wild ancestors (Miklosi et al., 2003), and that different results might
358 be obtained with feral or wild individuals. This is an area worthy of further investigation
359 in future studies. Although there was a sex bias towards males in the available
360 population, all cats were neutered and we did not set out to assess sex effects. We
361 cannot therefore make a firm conclusion about the bias that might exist in entire animals
362 or what contributed to the reverse preference of one of the males. This consistent
363 individual result is in sharp contrast to the data from the other animals. It may simply be
364 the result of natural population variation; however, it might reflect differences in that
365 individual's previous experience. It would also be interesting to investigate whether it is
366 of clinical significance, for example, whether or not these cats more likely to respond to
367 the chemical signals of other cats in their environment with urine spraying (Natoli,
368 1985). It is well known that some cats seem to start urine spraying in response to small
369 changes in their environment, that might be associated with changes in its olfactory
370 quality (Nielson, 2009), but other cats, even within the same household do not respond
371 in the same way. This raises the intriguing hypothesis that sensory bias in the cues used
372 for orientation may underpin individual differences in response to potential stressors.
373 This hypothesis could easily be tested by using the procedure described here on a
374 matched pairs population from within the same home of spraying and non-spraying
375 subjects. It is recognised that there are many reasons why a cat may spray (Nielson,

376 2009) and so it would be important to define the phenotype of spayers quite precisely to
377 ensure they are individuals who appear to be responding to olfactory changes in the
378 environment.

379 The odour alone test showed that the cats were also able to discriminate between
380 the stimulus odours when presented in isolation, revealing that they had the potential to
381 use olfactory cues in the cue-conflict tests, but chose to use visual ones. This ability to
382 use multiple cue features but preferentially use one over another has been found in other
383 species in a range of contexts. For example, pigeons tested on colour-shape compound
384 stimuli, used colour to make their discrimination (Wilkie and Mason, 1976). Likewise,
385 cats trained with separate stimulus sets and tested with compound stimuli contrasting
386 size, shape and brightness, appeared to respond most to the brightness cue (Hara and
387 Warren, 1961). Indeed most previous sensory discrimination and learning work on cats
388 has tended to focus on purely visual stimuli, and the current work adds further weight to
389 the importance of this sensory modality in this species, despite its excellent sense of
390 smell.

391

392 **5. Conclusion**

393 In conclusion, cats are able to attend to a range of stimulus features in order to
394 make a discrimination and when presented with an intermodal visual-olfactory stimulus,
395 the visual modality appears to predominate for most cats. However, the cat that used
396 odour did so at a significant level, suggesting that different individuals attend to
397 different elements of a stimulus. This suggests that individual differences could play a
398 key role in this type of learning; further investigation of underlying causes of this is
399 necessary as is the investigation of the clinical implications.

400

401

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518 necessarily imply analytic processing; evidence from pigeons (*Columba livia*), squirrels
519 (*Sciurus carolinensis*) and humans (*Homo sapiens*). *J. Comp. Psychol.* 123, 391-405.
520

520 Figure captions

521

522 Fig. 1. Experimental visual stimuli reflectance spectra

523

524

525 Fig. 2. Diagrammatic representation of experimental apparatus. Note the compound
526 stimulus was suspended within the frame of a cat flap with the flap removed at point X.

527

528 Fig. 3. Cats' mean stimulus set 1 and set 2 training performance for the discrimination
529 task.

530 The X axis represents the session number and the Y-axis represents the number of
531 correct choices out of 10 trials per session. Error bars indicate ± 1 standard error.

532

Table 1. Experimental odours and description according to Laska and Teubner (1999)

Compound	Chemical description	Conc. (g/L) in diethyl phthalate	Odour as perceived by humans	Masses/volumes required per 25mL
(1R,2S,5R)-(-)-menthol	Monocyclic terpene-alcohol	66.7	Peppermint, strong cooling	1.6675g
(1S,5S)-(-)- α -pinene	Bicyclic terpene-hydrocarbon	86.0	Pine-like	2460 μ L
R-(-)-carvone	Monocyclic terpene-ketone	96.0	spearmint	2503 μ L
R-(+)-limonene	Monocyclic terpene-hydrocarbon	421.5	orange	12,515 μ L
S-(-)- β -citronellol	Acyclic terpene-alcohol	85.4	Geranium oil-type	2494 μ L
(+)-fenchone	Bicyclic terpene-ketone	94.5	Camphoraceous, sweet	2500 μ L
Diethyl phthalate 99% Acros Organics (Diluent)			No odour	To 25mL total volume

Table 2. Stimulus set 1 and Stimulus set 2 pairings. * This stimulus set was reused for Lilly as Leon did not reach criterion with it.

Subject	Stimulus set 1	Stimulus set 2
1. Ziggy	Green/Carvone (S+) vs. Purple/Limonene (S-)	Red/Menthol (S+) vs. Blue/Pinene (S-)
2. Tigg	Brown/Citronellol (S+) vs. Yellow/Fenchone (S-)	Green/Limonene (S+) vs. Red/Pinene (S-)
3. Sammy	Blue/Carvone (S+) vs. Green/Citronellol (S-)	Red/Fenchone (S+) vs. Yellow/Menthol (S-)
4. Paddy	Brown/Limonene (S+) vs. Yellow/Carvone (S-)	Purple/Pinene (S+) vs. Blue/Menthol (S-)
5. Max	Green/Menthol (S+) vs. Red/Carvone (S-)	Blue/Limonene (S+) vs. Brown/Pinene (S-)
6. Leon	Yellow/Citronellol (S+) vs. Purple/Fenchone (S-)	Green/Pinene (S+) vs. Brown/Menthol (S-)
7. Lily*	Yellow/Citronellol (S+) vs. Purple/Fenchone (S-)	Green/Pinene (S+) vs. Brown/Menthol (S-)
8. Mumtas	Purple/Carvone (S+) vs. Yellow/Pinene (S-)	Green/Fenchone (S+) vs. Blue/Citronellol(S-)

Table 2. Stimulus set 1 and Stimulus set 2 pairings. * This stimulus set was reused for Lilly as Leon did not reach criterion with it.

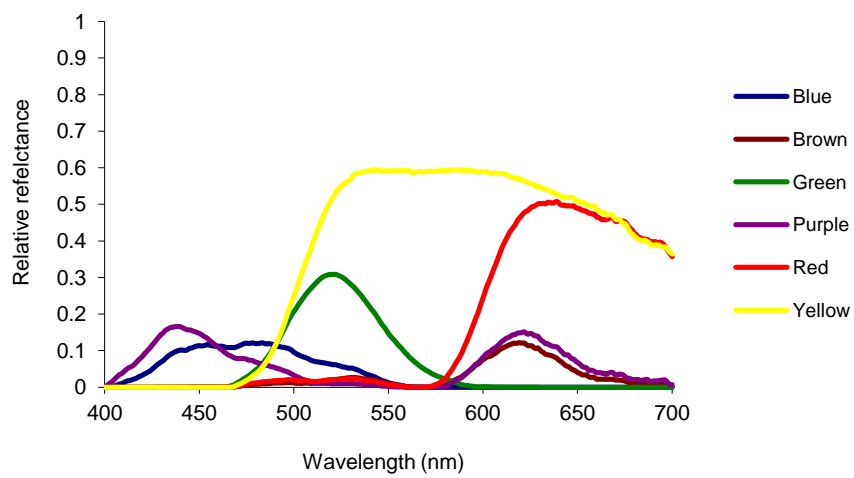
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Table 3. Conflict test data. Test data is presented in terms of the choice of the visual S+; If an animal chose the visual S+ for each trial it would receive a score of 12, if it choice the odour S+ on each trial, it would receive a score of 0. The values in brackets denote the P-values after correction using the false discovery rate.

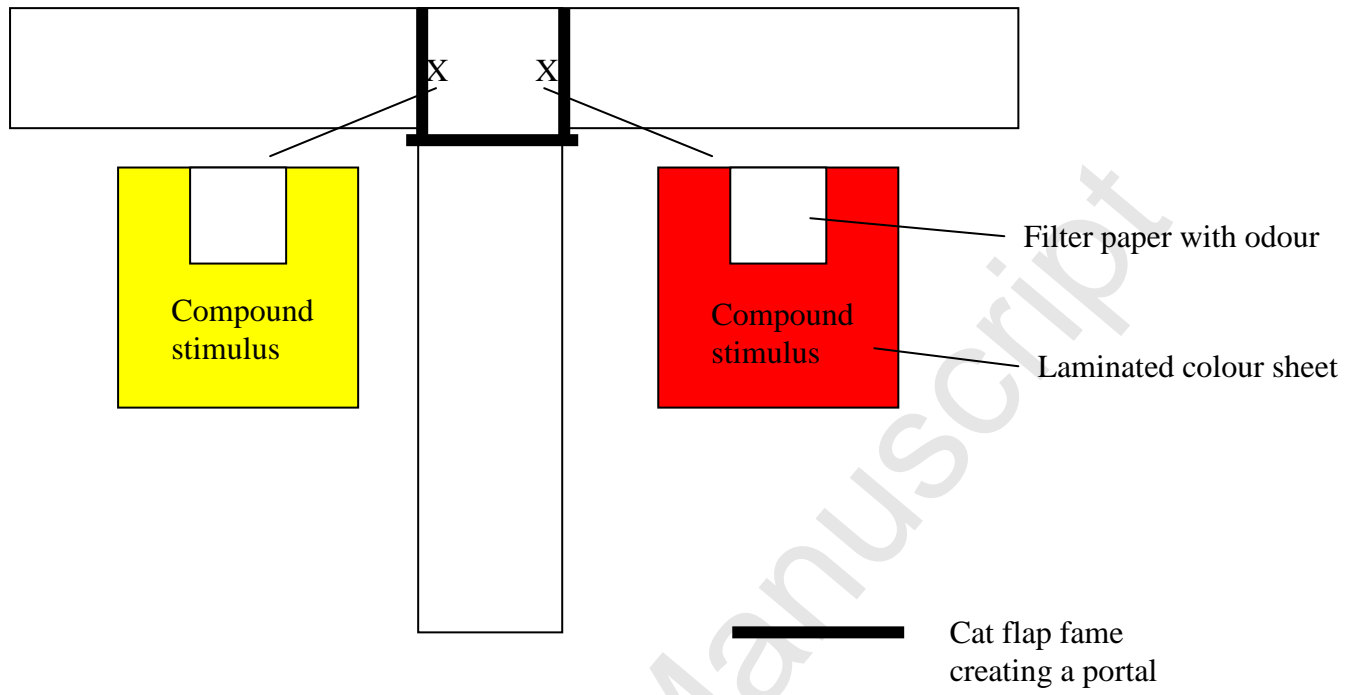
Cat	Choice of visual S+ cue (Stimulus set 1)	Choice of visual S+ cue (Stimulus set 2)	Significance (P with FDR)
1 Ziggy	10	11	0.022 (0.026)
2 Tigg	3	1	0.019 (0.026)
3 Sammy	10	11	0.022 (0.026)
4 Paddy	11	11	0.006 (0.018)
5 Max	11	11	0.006 (0.018)
8 Mumtas	9	11	0.076 (0.076)

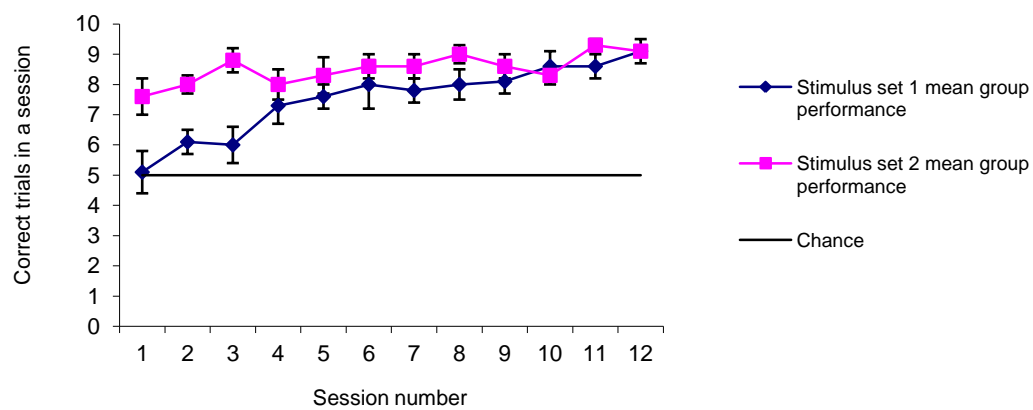
Table 4. Odour only test data. . Test data is presented in terms of the choice of the positive odour stimulus. The values in brackets denote the P-values after correction using the false discovery rate.

Cat	Correct choice (Stimulus Set 1)	Correct Choice (Stimulus Set 2)	Significance (P with FDR)
1 Ziggy	11	11	0.006 (0.012)
2 Max	11	12	0.003 (0.031)
4 Paddy	11	11	0.006 (0.012)
8 Mumtas	11	9	0.076 (0.076)



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Conflict of interest statement

The authors declare no conflict of interest with the work

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