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Formation of an olfactory search image for explosives odours in sniffer dogs

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Running title: olfactory searching in dogs. Gazit et al.

Total number of words: 4,897.

This research reports portions of a doctoral dissertation submitted by Irit Gazit to the University of Tel Aviv.

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Abstract

The term “search image” refers to an animal’s heightened ability to detect a specific cryptic prey following experience with that prey. Formulated in 1960 by Tinbergen, the search image concept has been the subject of much research, albeit almost entirely based on visual search cues in birds of prey. Given the theoretical and practical importance of this concept for foraging or searching in general, we set out to investigate whether dogs could form an olfactory search images for explosive odours. Seven experienced explosives detector dogs were **first** tested for their ability to detect 30 grams of the explosives TNT, C4 or PENT placed in various containers randomly distributed along a 300 meter limestone track. In consecutive stages of the experiment, we altered the relative percentages of the three explosives. The results showed that the percentage of TNT containers detected by the dogs increased in trials that followed placing of a high percentage of TNT relative to other explosives and decreased in trials that followed placing of a relatively low percentage of TNT containers. The percentage detection of C4 and PETN was not influenced by their relative abundance at any stage. Overall, these results suggest that dogs can form an olfactory search image that might aid in prey/target detection.

Keywords: dog, explosives, odour, search image, perceptual learning, learning.

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General introduction

49 The term “search image” was first used by Von Uexkull (1934; in Shettleworth 1998) who
50 described looking for a familiar earthenware water jug and not seeing the glass one that had
51 replaced it. He attributed this to the fact that he had formed a mental image of the
52 earthenware jug as a guide in his search for water. Von Uexkull suggested that animals too
53 possess a mental image of a prey item that enhances their ability to detect matching items
54 (Shettleworth 1998). This concept of a mental search image was used by Tinbergen (1960) to
55 explain the fact that the relative percentages of different prey species collected by tits differed
56 from their relative percentages in the field. Tinbergen found that the tits overselected prey
57 with which they were familiar. He postulated that the birds had learned to recognize specific
58 characteristics of a given prey and that this learning resulted in a search image that facilitated
59 detection of the familiar prey (Tinbergen 1960 cited in Croze 1970). Since that seminal
60 observation, research on the search image can be divided into two types: field and semi-field
61 studies using free-flying birds (e.g. Tinbergen 1960; Allen & Clarke 1968; Croze 1970;
62 Lawrence 1985; Lawrence 1986); and controlled experiments in operant chambers (e.g.
63 Pietrewicz & Kamil 1981; Bond 1983; Plaisted & Mackintosh 1995; Langley et al. 1996).
64 The great majority of the field studies have concentrated on aspects such as how do the birds
65 learn to detect prey over a time-scale of days, weeks and even seasons (e.g. Tinbergen 1960;
66 Croze 1970; Lawrence 1986) The major conclusion of these studies is that many birds
67 develop a search image over a time period of at least days and that this search image is stable
68 from day to day.

69 In contrast to the field studies, the laboratory experiments, with the notable exception of
70 Pietrewicz and Kamil (1981), have been primarily concerned with the effects of runs, i.e. of
71 multiple encounters over a short time span with one prey type, on the relative probability of
72 selecting that specific prey as opposed to an alternative prey type. In general, the laboratory

73 studies have found that runs of one prey type improve the ability to detect such prey but can
74 also interfere with the ability to detect prey of a different type (e.g. Bond & Kamil 1999).
75 According to most laboratory studies, and contrasting with the findings of field research,
76 search images have generally been found to be transient, lasting from a few seconds to a few
77 minutes. For example, Dawkins (1971), Langley et al. (1996) and Gendron (1986) all found
78 that the search image lasted only minutes. Plaisted and Mackintosh (1995) reported only very
79 slight improvement from day 1 to day 2. The common and accepted explanation for these
80 laboratory findings is that a run of one prey type momentarily improves the probability of
81 selecting prey of that type via selective attention to those targets that appeared in the run.

82 In summary, field studies on the search image have been more concerned with its learning or
83 development and have found stable long-term search images. Laboratory studies, in contrast,
84 have focused on improved performance as a result of runs, after the target characteristics of
85 both prey types have already been learned, and have generally found very temporary search
86 images that are dependent on short-term runs of different target types.

87 If the search image concept remains confined to studies showing selective attention in birds
88 as revealed by the runs effect, then its usefulness as a general concept will be limited.

89 Consequently, it is important to determine the usefulness of this concept beyond that of
90 granivorous birds searching for visible prey. It is possible indeed, that both the learning and
91 long-term maintenance of search images may be a general adaptation of predators searching
92 for a type of prey that is infrequently encountered. Acquisition of long-lasting search images
93 could be more useful to a foraging predator than the brief shifts in attention found as a result
94 of runs in laboratory experiments. Thus it is important to investigate both the formation of a
95 search image and the effects of runs in species other than birds and with senses other than
96 vision.

97 Olfaction may be used for a search image in mammals. However, to date very few studies
98 have addressed the development of an olfactory search image or the effects of runs of odour
99 on prey choice. In support of an olfactory search image, Nams (1997) found that skunks
100 improved day-by-day their ability to detect a food odour. This occurred even when the
101 animals were exposed to the food odour only once per day. However, Nams did not use two
102 types of prey and therefore could not determine if there were any effects of runs.
103 Demonstration of an olfactory search image in other mammals would greatly enhance the
104 power and scope of the search image concept. Here we investigate the possible acquisition of
105 an olfactory search image in well trained explosives detection dogs.

106 There are several advantages to using explosives detection dogs in such an investigation.
107 First, dogs have proven olfactory capabilities and are known to use olfaction while hunting.
108 Second, the dogs we used were already well trained in searching for specific odours and were
109 very familiar with the experimental paradigm, i.e. searching a track for olfactory stimuli, and
110 therefore needed no additional prior training. Moreover, the dogs were already familiar with
111 searching large outdoor areas off leash. The dogs' previous training of searching along the
112 length of the track enabled us to place sequences of odours in a manner analagous to that of
113 "runs" in laboratory simulations. Finally, determining the dogs' ability to form an olfactory
114 search image could have important practical consequences for the utilization and
115 maintenance of explosives detection dogs.

116 We thus designed a series of experiments to determine whether dogs can develop a search
117 image for the odour of explosives. Specifically, we asked whether extensive training with one
118 explosive would improve their ability to detect that explosive and whether it would interfere
119 with their ability to detect the odours of other explosives. In the work reported below, we
120 used dogs trained to detect three commonly used explosive odours. Following determination
121 of a stable baseline detection percentage for each odour, we investigated the effects of

122 varying the relative probabilities of encountering the explosives odours (runs effect) on the
123 percentage of detection.

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125 Material and Methods

126 The current study used sniffer dogs of the breeds Malinois (4 dogs) and Labrador retriever (3
127 dogs) trained for explosives detection (Table 1). All the dogs were trained to search for
128 hidden olfactory stimuli using standard procedures (Mitchell 1976). They were taught to sit
129 next to any explosive odour they found and were reinforced with a few pieces of commercial
130 dog chow. A qualified dog searched the area off leash while the handler followed 50 – 100
131 meters behind it. The dogs were never punished for misses or false positives. Immediately
132 prior to this experiment, the dogs had had two years of ongoing experience with the explosive
133 C4. They had also been previously trained to detect the other two explosives used here, TNT
134 and PETN, but had not encountered them for two years before this experiment. Previous
135 research had revealed that there were no differences between Malinois and Laborador
136 retrievers in their ability to search for and detect explosives (McLean 2001).

137

138 General procedures

139 The experiment took place along a 2100m soft limestone track, four meters wide bordered by
140 tall grass on both sides. The track was divided into seven equal 300 meter sections. In order
141 to avoid odour contamination by previous dogs on the same track, each dog searched one
142 different section per day. The dogs were required to detect 30g of C4 (composition C4: RDX
143 + polyisobutylene + di(2-ethylhexyl)sebacate + fuel oil), TNT (2,4,6-Trinitrotoluene) or
144 PETN (Pentaerythritol tetranitrate). For practical reasons we did not attempt to equate the

145 probability of detection between the three explosives by manipulating the relative weight of
146 each sample.

147 In a pilot study we systematically manipulated the amount of explosives and found that 30g
148 was sufficient for detection but required active search by the dog. Prior to the start of the
149 present study the dogs received several weeks experience with 30 gram amounts of all three
150 explosives. The explosives were placed in a wide variety of containers (glass salt shakers
151 with metal lid, plastic soap-holders, small metal cans and wooden boxes) to ensure that the
152 dogs responded to the explosive odour rather than the container odour. As controls we used
153 dummy containers identical to those with the explosives but filled with either a wide range of
154 odour sources (such as soil, sugar, coffee, and bread) or left empty.

155 The containers were placed in different locations before each trial. Each dog performed only
156 one trial per day, each time on a different one of the seven 300 meter sections, thus
157 preventing it from using memory of the explosives found on the previous days. In order to
158 avoid foot trail odour cues, the explosives containers and dummies were thrown from the
159 window of a car moving slowly along the track. The containers usually came to rest one to
160 two meters into the vegetation on each side of the track. If the container landed in a too
161 visible position, we replaced it. Neither the dogs nor their handlers observed the placement of
162 the containers, nor were the handlers informed as to their location. In addition, the containers
163 were not visible to the handler walking along the path. The containers were placed along each
164 track 30 min prior to the search.

165 A video camera (Sony, E-65) was used to film the trials. The video tapes enabled post-factum
166 analysis of the dog's behaviour while searching for explosives. A digital temperature and
167 humidity gauge, $\pm 1^{\circ}\text{C}$ and $\pm 3\%$ accuracy, recorded temperature and humidity during the
168 experiment and a windmeter, Davis Wind Wizard, was used to determine both the direction
169 and speed of the wind during the trials.

170 In the standard testing procedure each dog was brought to the start of the path by its
171 handler.. The dog's leash was removed and the dog was sent forward to search the track. The
172 experimenter walked about 5 to 10 meters behind the dog while observing and recording its
173 behaviour. The dogs never responded to the presence of the experimenter. The handler would
174 advance behind the dog while maintaining a distance between 50 and 100 meters. If the dog
175 indicated the presence of an explosive the experimenter would signal to the handler to
176 reinforce the dog. If the dog missed a target the experimenter noted the fact but did not
177 inform the handler. If the dog made a false positive response the handler recalled it and sent it
178 to continue searching. The dog would continue searching the track until the handler was
179 instructed by the experimenter to stop the search. A normal search, including detection and
180 reinforcement, lasted approximately ten minutes.

181 Specific Procedures

182 We first established the baseline detection percentage for 30 grams of each explosive when
183 the explosives were equally and randomly distributed (stage 1). The probability of detection
184 for each odour was determined by testing the dogs for eight successive trials with the three
185 explosives, with which they were already familiar. In each trial three dummy containers and
186 between five and eight explosives containers with either PETN, TNT or C4 (totalling an
187 equal number of each explosive over the 8 trials) were randomly distributed on a 300 meter
188 section of track as explained above. Each dog was sent to search the path using the above-
189 mentioned standard procedure.

190 Next we established whether dogs develop an olfactory search image by exposing each dog
191 to TNT for ten consecutive trials and measuring improvement in detection as the percentage
192 of containers found (stage 2). At each trial we used eight containers with TNT and three
193 dummy containers randomly distributed as explained above. If dogs do form an olfactory
194 search image we would expect the detection rate to increase with the trials.

195 Further, to assess whether exposure to a particular odour leads to increased detection of that
196 familiar odour and decreased detection of a less familiar odour we tested the dogs with low
197 frequencies of C4 and PETN separately and compared the outcome with the baseline
198 detection rate (stage 3).

199 We thus first gave the dogs ten trials on paths containing six TNT containers, two C4
200 containers and three dummy containers, followed by ten trials with only TNT in order to re-
201 establish a search image for TNT, and finally ten trials on paths with six TNT, two PETN and
202 three dummy targets. All containers were randomly distributed as described above. If the
203 formation of a search image inhibits detection of rarer odours we would expect the detection
204 rates for C4 and PETN to decrease from the baseline level.

205 Finally, we tested whether the presumptive search image is weakened following exposure to
206 an alternative odour. If so, a dog previously exposed to a high percentage of TNT should
207 show a decreased detection rate of that target following exposure to a high percentage of
208 alternative odours (C4 or PETN). We thus tested the dogs for eight trials on paths containing
209 six PETN targets, two TNT targets and three dummies.

210 The data were analysed in terms of the probability of detection. Percentages were converted
211 using the arcsine transformation recommended by Weiner (1962). All data were analysed
212 through STATISTICA (Copyright StatSoft inc. 1984-2004) software using parametric
213 statistics. For each dog we calculated the percentage detections over the entire trials of each
214 stage. We then used either ANOVA or paired t-tests to compare between stages.

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Results

220 The baseline detection rate differed significantly for the three explosives (TNT = 80.03% ±
221 3.21, PETN = 88.59% ± 3.54, C4 = 92.07% ± 2.85; ANOVA $f_{2,6} = 3.54$, $p = 0.05$). (Table 1).
222 Pairwise post-hoc comparisons (series of paired T tests) showed that this difference was due
223 to C4 being detected at a higher rate than TNT (C4 vs TNT $t = 4.16$, $df = 6$, $p = 0.005$; C4 vs
224 PETN $t = 1.02$, $df = 6$, $p = 0.34$; TNT vs PETN $t = 1.99$, $df = 6$, $p = 0.09$). We found no significant
225 differences between individual dogs (ANOVA, $f_{2,6} = 1.66$, $p = 0.2$) and no positive responses to
226 either empty containers or those containing non-explosives odours. These results show that
227 the dogs had learned the task and responded only to the odours of the three explosives. In
228 addition, they show that TNT was significantly more difficult to detect than C4. The lower
229 detection rate of TNT suggested that it would be the best candidate for determining whether
230 the dogs are able to form an olfactory search image.

231 When the dogs were continually trained on only TNT their detection rate increased
232 significantly over time from a baseline detection rate of 80.03%±3.21 to a final rate of
233 90.35%±1.16 (paired T-test $t = 2.8$, $df = 6$, $p = 0.03$) (Table 1). As in the previous stage, there
234 were no positive responses to non-explosive odours. This showed that extensive training with
235 only TNT had resulted in the development of a search image for this explosive, as seen by the
236 improvement in the percentage of its detection.

237 Next we tested whether improved detection of the high-probability target is accompanied by a
238 concomitant decrease in detection of the low-probability target. Exposure to 10 trials with
239 75% TNT targets and 25% C4 targets did not result in a significant decrease in the detection
240 of C4 (92.86%±4.95, as compared to the baseline at 92.07%±2.85; 2-tailed paired t-test
241 $t = 0.55$ $df = 6$, $p = 0.6$). The percentage of TNT detection increased slightly (86.22%±2.04 as
242 compared to the baseline at 80.03%±3.21), but this difference was not significant (2-tailed t-
243 test, $t = 1.56$, $df = 6$, $p = 0.08$; Fig. 1, Table 1).

244 Please insert Fig.1

245 Following another 10 trials with only TNT the dogs were given 10 trials with 75% TNT and
246 25% PETN. Although there was no significant decrease compared to the baseline detection
247 rate of PETN, (baseline rate of PETN = $88.59\% \pm 3.54$ vs $91.29\% \pm 3.27$, two-tailed paired t-
248 test, $t=1.09$, $df=6$, $p=0.31$) there was a significant increase in detection of TNT when
249 compared to the baseline ($93.74\% \pm 2.41$ vs baseline of $80.03\% \pm 3.21$, two-tailed paired t-test,
250 $t=3.38$, $df=6$, $p=0.01$). (Fig.2, Table 1). These results suggested that the development of a
251 search image for TNT was not accompanied by decreased detection of either C4 or PETN.

252 Please insert Fig.2

253 If the increased detection of the high-probability TNT was indeed due to the formation of a
254 search image, then reducing the percentage of TNT should now reduce its detection. We
255 tested this in stage 4 by reversing the relative probabilities of PETN and TNT. Instead of 6
256 TNT and 2 PETN used in stage 3, the dogs were trained with 6 PETN and 2 TNT (a reduction
257 of TNT from 75% to 25%). Detection percentages at the beginning of stage 4 were higher for
258 both explosives than in the previous stages. However, whereas PETN detection percentage
259 remained almost stable at around 100% throughout all stage 4 trials, TNT detection
260 percentage was highest (100%) for the three first trials and then gradually decreased to 66%
261 detection (Fig. 3). This was the lowest detection percentage for TNT found during the entire
262 study (Fig.1). ANOVA for repeated measures showed that the decrease in detection of TNT
263 as a function of trial number was significant ($f_{7,43}=3.8$ $f<0.005$). These results strongly
264 suggest that a search image had been created for TNT.

265 Please insert Fig. 3

266 Please insert Table 1

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Discussion

270 Our results strongly suggest that dogs form an olfactory search image. When exposed to ten
271 trials with only TNT, detection rate of TNT significantly increased in the following trials.

272 Changing the percentage of C4 or PENT targets, however, had no effect on the probability of
273 their detection, which remained high throughout. We further found that when the percentage
274 of TNT targets was reduced relative to the percentage of PETN targets the detection rate of
275 TNT targets decreased. This suggests that once a search image for a specific target has been
276 developed, it is maintained for only as long as the probability of encountering that target is
277 high.

278 Our results thus support the formation of an olfactory search image in dogs, since we found
279 an improvement in the ability of the dogs to detect the target TNT as a result of extended
280 experience with that target, as well as a reduction in the probability of detection of TNT when
281 its probability of occurrence was reduced. This confirms and extends the findings of Nams
282 (1997), who showed that skunks greatly improved their ability to detect and orient to a food
283 odour following repeated training with that odour. Indeed, improvement with practice has
284 been found in most of the field studies (Tinbergen 1960; Croze 1970; Lawrence 1985). This
285 improved detection as a result of learning the target characteristics was also found in field
286 studies investigating foraging in birds (Tinbergen 1960, Allen & Clarke 1968; Lawrence
287 1985) and is a component in the development of the search image for any target. The
288 sensitivity of the search image to changing target abundance is another component of the
289 search image as formulated by Tinbergen, and as confirmed in many field studies on foraging
290 in birds (e.g. Tinbergen 1960; Allen & Clarke 1968; Lawrence 1985).

291 Some of our findings, however, do not concur with the current definition of formation of an
292 olfactory search image. First, we found that even when the percentage of PETN targets was
293 increased, there was no increase in its detection. This is inconsistent with the formation of a

294 search image, but can be explained by a ceiling effect. Since the baseline detection percentage
295 of PETN was 88.6%, it would be difficult to find a statistically significant increase in its
296 detection. More troublesome to our contention that the dogs developed an olfactory search
297 image was the lack of decreased detection of either PETN or C4 when they were the low-
298 probability target. However, although the search image concept predicts a decrease in
299 detection of a less encountered target, the failure to find such a decrease is not unusual in the
300 search image literature. Bond & Riley (1991), Tucker & Allen (1993) and Bond & Kamil
301 (1999) have suggested under what situations a decrease may not be found. Bond & Kamil
302 (1999), for example, summarizing the literature on the effects of low target probability on
303 detection rate, concluded that if two targets initially differ in detectability, then a run of the
304 more detectable target will reduce the probability of detection of the less detectable target.
305 However, a run of the less detectable target will not decrease the probability of detection of
306 the more detectable target. This is consistent with our results. TNT was initially less
307 detectable than either PETN or C4, and a run of TNT did not reduce the probability of
308 detection of the more detectable PETN or C4. However a run of the more detectable PETN
309 did reduce the percentage detection of the less detectable TNT.

310 Another potential problem in the contention that our results are due to the formation of a
311 search image is the salient nature of our olfactory targets. Langley and others have suggested
312 that search images are formed only for cryptic targets (e.g. Langley et al. 1996). Since our
313 targets were relatively easy to detect, a search image should not have formed. However, it has
314 been suggested that the entire issue of crypsis in the formation of a search image needs to be
315 re-examined (e.g. Blough 2001). Gendron (1986) too suggested that crypsis is not essential.
316 He found the development of a search image even when using very conspicuous brown or
317 green pellets. Finally, the prototype observation on the search image concept was by Von
318 Uexkull (1934/1957 in Shettleworth 1998), who had failed to see the glass water jug on his

319 breakfast table that had replaced the familiar earthenware jug, even though a glass jug on a
320 table is not very cryptic. There are, therefore, other data showing that search images can be
321 formed for salient stimuli.

322 In our experiments we showed that dogs acquire and use an olfactory search image. These
323 results support the usefulness of the search image concept beyond that of birds searching for
324 visible prey. We suggest that the acquisition of the search image is part of the more general
325 concept of perceptual learning, where exposure to a stimulus improves the ability of the
326 subject to discriminate and detect that stimulus from the background (Goldstone 1998).

327 Although perceptual learning is usually studied with either visual or auditory stimuli, Wilson
328 and Stevenson (2003) have made a very strong case for the perceptual learning of olfactory
329 stimuli in a variety of species.

330 After an animal has acquired a search image for a specific target, its maintenance seems to be
331 dependent on the relative target probability. We have shown that the dogs' probability of
332 detection of TNT was dependent on the relative percentage of TNT targets. This result, which
333 is analogous to that found in foraging birds, supports a two-stage search image. After an
334 animal acquires the search image, another mechanism, possibly selective attention, is
335 responsible for its continued maintenance. This concept seems to be in agreement with
336 Tinbergen's original formulation of the search image concept.

337

338 Acknowledgement

339 We gratefully acknowledge the constructive comments of the anonymous reviewers and
340 especially the associate editor. We also thank Naomi Paz for her editorial skill and patience in
341 the preparation of the manuscript. We thank too the dog handlers and dogs for participating in
342 this study.

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References

345

1. Allen, J. A. & Clarke, B. 1968: Evidence for apostatic selection by wilde

346

Passerines. *Nature* **220**, 501-502.

347

2. Blough, P. M. 2001: Cognitive strategies and foraging in pigeons. In: R.G.

348

Cook (Editor), *Avian visual cognition* [on line]. Available:

349

www.pigeon.psy.tufts.edu/avc/pblough/

350

3. Bond, A. B. 1983: Visual search and selection of natural stimuli in the pigeon:

351

The attention threshold hypothesis. *Journal of Experimental Psychology:*

352

Animal Behaviour Processes **9**, 292-306.

353

4. Bond, A. B. & Riley, D. A. 1991: Searching image in the pigeon: A test of

354

three hypothetical mechanisms. *Ethology* **87**, 203-224.

355

5. Bond, A. B. & Kamil, A. C. 1999: Searching image in blue jays: Facilitation

356

and interference in sequential priming. *Animal learning & behavior* **27**, 461-

357

471.

358

6. Croze, H. 1970: Searching image in Carrion crows. *Zt.Tierpsychol.* **5** 1-86.

359

7. Dawkins, M. 1971: Shifts of "attention" in chicks during feeding. *Animal*

360

Behaviour **19**, 575-582.

361

8. Gendron, R. P. 1986: Searching for cryptic prey evidence for optimal search

362

rates and the formation of search images in quail *colinus-virginianus*. *Animal*

363

Behaviour **34**, 898-912.

364

9. Goldstone, R. L. 1998: Perceptual learning. *Annual Review of Psychology* **49**,

365

585-612.

366

10. Langley, C. M., Riley, D. A., Bond, A. B. & Goel, N. 1996: Visual search for

367

natural grains in pigeons (*Columba livia*): search images and selective

- 368 attention. *Journal of Experimental Psychology: Animal Behaviour Processes*
369 **22**(2), 139-151.
- 370 11. Lawrence, E. S. 1985: Evidence for search image in blackbirds *Turdus merula* L.:
371 long term learning. *Animal Behavior* **33**, 1301-1309.
- 372 12. Lawrence, E. S. 1986: Can great tits *parus-major* acquire search images. *Oikos*
373 **47**, 3-12.
- 374 13. McLean, I. 2001: Designer dogs: Improving the quality of mine detection
375 dogs. Geneva Internatioanal Center for Humanitarian Demining.
- 376 14. Mitchell, D. S. 1976: Training and employment of land mine and booby trap
377 detector dogs. Final technical report, vol.2. United States Army Mobility
378 Equipment Research and Development Command. Ft. Belvoir, Virginia
379 22060. Contract No, DAAKO2-73-C-0150.
- 380 15. Nams, V. O. 1997: Density depended predation by skunks using olfactory
381 search images. *Oecologia* **110**, 440-448.
- 382 16. Pietrewicz, A. T. & Kamil, A. C. 1981: Search images and the detection of
383 cryptic prey: an operant approach. In: *Foraging behavior: Ecological,*
384 *ethological, and psychological approaches*, 1st edn (Kamil, A.C.& Sargent, T.
385 D., eds.). New York, London: Garland STPM Press, pp. 311-331
- 386 17. Plaisted, K. C. & Mackintosh, N. J. 1995: Visual search for cryptic stimuli in
387 pigeons: implications for the search image and search rate hypotheses. *Animal*
388 *Behavior* **50**, 1219-1232.
- 389 18. Shettleworth, S. J. 1998: *Cognition, Evolution, and Behavior*. Oxford
390 University Press, New-York.

- 391 19. Tinbergen, L. 1960: The natural control of insects in pine woods. 1. Factors
392 influencing the intensity of predation by song birds. Archives Neerlandaises
393 de zoologie **13**, 265-343.
- 394 20. Tucker, G. M. & Allen, J. A. 1993: The behavioural basis of apostatic
395 selection by humans searching for computer-generated cryptic 'prey'. Animal
396 Behaviour **46**, 713-719.
- 397 21. Wilson, D. A. & Stevenson, R. J. 2003: Olfactory perceptual learning: the
398 critical role of memory in odor discrimination. Neuroscience Biobehavioural
399 Review **27**, 307-328.
- 400 22. Winer, B. J. 1962: Statistical principles in experimental design. McGraw-hill,
401 Book company, NY.
- 402

402 Table 1. Changes in detection probability by dogs throughout the stages.

	Breed	Sex	Age (Years)	Stage 1			Stage 2			Stage 3	
				TNT	C4	PETN	TNT	TNT	C4	TNT	PETN
Rondo	Belgian Malinois	Male	3	66.66	87.50	85.70	91.60	88.88	100.00	94.10	83.30
Leon	Belgian Malinois	Male	4.3	73.33	88.20	93.33	90.74	83.33	66.66	85.70	100.00
Bella	Belgian Malinois	Female	3.3	80.00	100.00	88.88	90.74	77.77	100.00	100.00	100.00
Sonia	Belgian Malinois	Female	5	83.33	84.60	70.00	92.64	88.88	100.00	100.00	90.00
Meshi	Labrador retriever	Female	2.5	78.94	84.20	93.33	83.90	88.23	100.00	88.88	85.70
Stu	Labrador retriever	Male	5.5	84.61	100.00	88.88	89.74	94.11	83.33	100.00	80.00
Ben	Labrador retriever	Male	6	93.33	100.00	100.00	93.10	82.35	100.00	87.50	100.00
Mean				80.03	92.07	88.59	90.35	86.22	92.86	93.74	91.29
SE				3.21	2.85	3.54	1.16	2.04	4.95	2.41	3.27

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Figure Legends

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406 Figure 1. Detection percentages of TNT and C4 at baseline and after posited TNT search
407 image (S.I) formation.

408

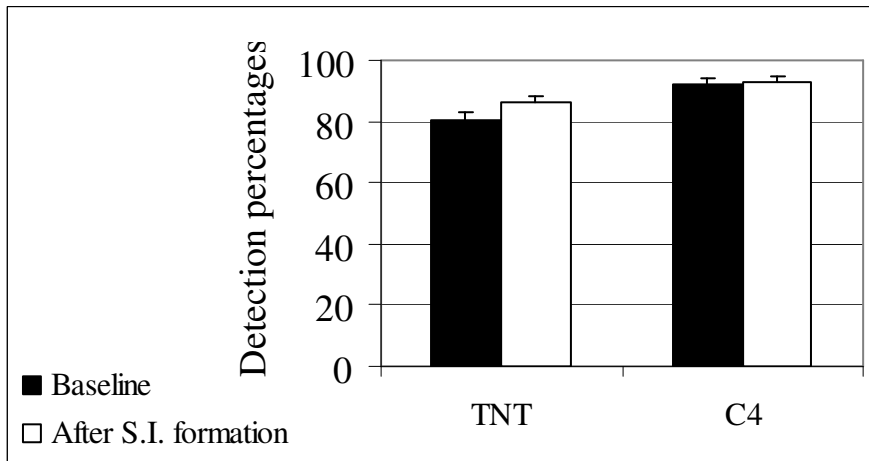
409 Figure 2. Detection percentages of TNT and PETN at baseline and after posited TNT search
410 image (S.I) formation. ** $p < 0.01$.

411

412 Figure 3. TNT and PETN mean detection percentages \pm SE for all dogs at every trial (1 to 8),
413 after switching of explosive type frequencies.

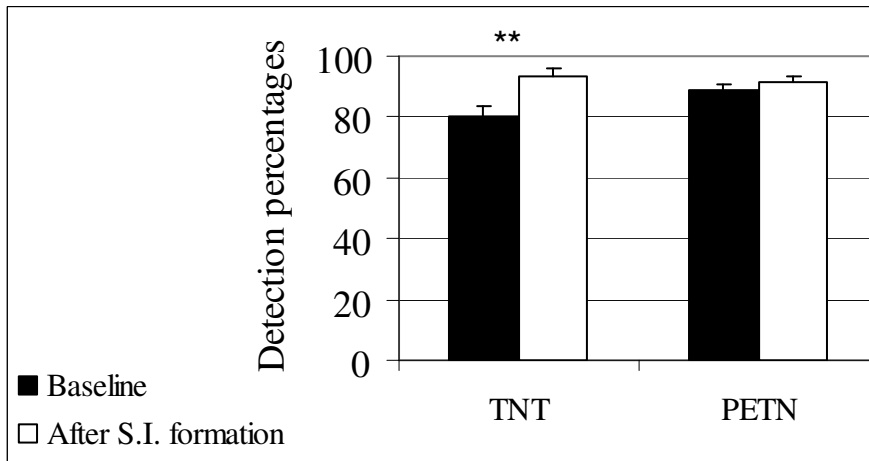
414

414 Fig. 1



415

416 Fig. 2

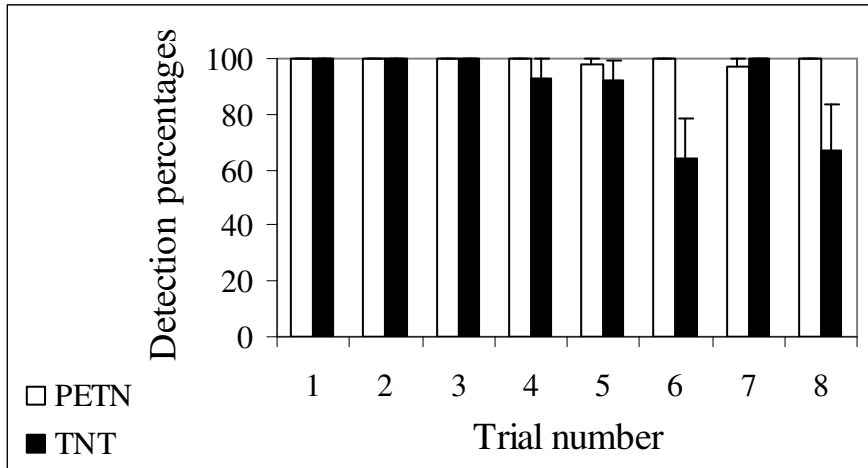


417

418 Fig. 3

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