Animal Behaviour 90 (2014) e1–e6

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Forum

Do olfactory stimuli provide positional information for home-oriented avian navigation?

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ARTICLE INFO

Article history:
Received 7 November 2013
Initial acceptance 13 December 2013
Final acceptance 19 December 2013
Available online 23 February 2014
MS. number: 13-00934

Keywords:
homing pigeon
navigational map
olfaction

A large sample of coherent experimental results obtained with homing pigeons and other birds led to the conclusion that birds are able to find their way home from distant unfamiliar areas by deducing positional information from atmospheric trace gases carried by winds and perceived by olfaction (Gagliardo, 2013; Papi, 1986, 1989, 1991; Wallraff, 1990, 2001, 2004, 2005a, 2005b, 2010). Furthermore, it has been shown that the atmosphere actually contains navigationally exploitable spatial information (Wallraff, 2000a, 2013; Wallraff & Andreae, 2000).

With these statements, the title question is answered in the affirmative. A reader without previous knowledge of the matter would surely have expected the contrary. We can all smell, but none of us is able to imagine that airborne odours might be in any way helpful to find the way home from never experienced areas over hundreds of kilometres (not only against the wind, but even with tail winds). The unstable atmosphere appears utterly unsuitable to contain sufficiently stable long-ranging spatial configurations. Most likely it is this intuitive disbelief that has made the topic 'avian olfactory navigation' controversial over the past 40 years in spite of a long list of well-matched empirical findings (briefly enumerated in Wallraff, 2005b) which otherwise would have been accepted as evidence without difficulty.

Intuitive disbelief could be rationally substantiated if it were possible to avoid the above conclusion by presenting alternative interpretations of the empirical results on which the conclusion is based. Most convincing success would be achieved if homeward orientation by birds from unfamiliar areas could concurrently be explained in an alternative way without ignoring any of the existing results. Over decades of research, the latter aim has not been accomplished, but several attempts have been made to search for a possible alternative explanation of this or that particular experimental result without offering an alternative approach towards a solution of the homing problem. I have discussed and dismissed almost all such attempts (Wallraff, 1983, 1988, 1990, 2001, 2004, 2005a), but not yet the most recent one of Jorge, Marques, and Phillips (2009, 2010), who claim to have shown that the effect of odours on pigeon homing is not navigational, but merely activational. Atmospheric odours are thought to carry no navigationally usable spatial information, but activate an 'independent non-olfactory map system' (Jorge et al., 2010, p. 45) whose required sensory input remains unknown. At first glance, Jorge et al.'s results may actually suggest such an interpretation. However, the authors present their activation hypothesis merely in general terms without allotting clear content to it and without discussing its implications and consequences with respect to the birds' natural life. The present article aims to accentuate these consequences and thereby questions the rationale of Jorge et al.'s experiments. It also hints at the incompatibility of their results with a number of other findings which on their part go perfectly together.

In the following, I use abbreviated references: JMP09 and JMP10 stand for Jorge, Marques, and Phillips (2009) and (2010), JMP for both together; W2005a means Wallraff (2005a).

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http://dx.doi.org/10.1016/j.anbehav.2014.01.012

ACTIVATIONAL VERSUS NAVIGATIONAL EFFECTS OF ODOURS ON PIGEON HOMING

This is the kind of experiment whose interpretation is controversial: pigeons sitting during transport to and/or at an unfamiliar site distant from home in an airtight container ventilated with natural local air can and do perceive and evaluate navigationally exploitable signals of whatever kind. If they are released after some time with their olfactory epithelia anaesthetized, they orient towards home. In contrast, if the container had been ventilated with pure air lacking any natural environmental trace volatiles (either synthetic or filtered air), the pigeons are disoriented (e.g. Figures 7 and 8 in Wallraff, 2004, Figures 7.8, 7.9 and 7.11 in W2005a).

JMP accept that homeward orientation of pigeons from an unfamiliar area requires some sort of olfactory input, but not that the olfactory input from natural local air contains navigationally exploitable information. For what else, then, should the olfactory input be indispensable?

JMP claim to have shown that natural volatiles can be replaced by arbitrary 'nonsense' odours such as lavender, camellia, eucalyptus and/or jasmine, which do not provide any navigationally useful information. Actually, when the authors mixed some of these odours into the synthetic or filtered breathing air, the pigeons flew towards home. (In JMP10 the experimental design was unnecessarily more complicated, but this does not affect the basic conclusion; see below.) How can this perplexing outcome be explained?

The JMP answer is the 'activation hypothesis' which proposes that the pigeons' homing system requires (any or particular?) olfactory input in order to activate a navigational 'map' mechanism which itself does not require the sense of smell.

The Rationale of the Activation Hypothesis

The methods and results presented by JMP cannot fundamentally be criticized. The problem is: what do they tell us? The hypothesis trying to explain the outcomes and to draw reasonable conclusions comprises a number of problematic implications and consequences.

(1) The word activation induces the assumption that the process needing to be activated is usually sleeping. According to JMP10 (p. 46), however, 'access to natural odours activates the use of nonolfactory map cues'. Consequently, as pigeons in their normal life have permanent access to such odours, the use of nonolfactory map cues is permanently activated. Then, on what occasion should it be deactivated? Does lack of olfactory input (due to anosmia or purified air) imply the turning off of a mechanism that does not use olfactory input? What could the biological sense, that is, the adaptive value be of such an on-off switch, which in normal life hardly ever comes into action? This consideration alone makes the activation hypothesis contestable. Logically, it cannot simply mean that access to any (natural or artificial) odours activates the use of nonolfactory map cues, whereas prevention of such access blocks it. Even the experiments of JMP themselves indicate that more specific conditions must be involved.

(2) The different effects of using a filter versus not using a filter are hardly simple effects of no odour versus odour. Pigeons sitting in a box ventilated with artificial or charcoal-filtered air are hardly deprived of any olfactory input. The pigeons themselves and their excretions in the airtight boxes produce their own volatiles (see Figure 7.7 E versus D in W2005a) which, at least in part, people can easily smell. Owing to very slow air exchange in the JMP experiments, the quantitative portion of self-produced volatiles was probably much higher than that of trace volatiles in the free atmosphere. Nevertheless, this pigeon scent was obviously unsuited to make the presumed homing machinery work, whereas lavender and jasmine are concluded to do so. From this difference it follows that, under the activation hypothesis, the quality of the olfactory input can hardly be irrelevant.

(3) On the other hand, if pigeons were insensitive to their own scent or became insensitive because of adaptation, but were sensitive without adaptation to some natural airborne volatiles, this would be a particular specialization that would need to have a particular adaptive advantage (see next item).

(4) Apparently, not all natural odours are thought to activate the birds' homing system. From JMP09 and after consulting Phillips, Muheim, and Schmidt-Koenig (2006) in addition, the reader may understand that an effective odour must be unfamiliar to the pigeon, and thereby suitable to indicate that the pigeon is not at home. On this condition, pigeons sitting in a closed box ventilated with local air some 30 or 50 km east of their loft must be able to deduce from their olfactory input that they are not at home. Thus, they must be sensitive to airborne volatile compounds at extremely low concentrations and able to recognize tiny differences in their mixtures. The step from this formidable sensory and analytical capability to the somewhat higher level allowing recognition to be somewhere east of home is not very large. On this somewhat higher level, the remarkable sensitivity and discrimination power make sense. For a pigeon having a nonolfactory map being able to tell that it is some 30 or 50 km east of its loft, however, does it also make sense to have an extremely sophisticated apparatus that contributes only the redundant message that the bird is not at home?

(5) This message may appear clear to the bird if unfamiliar eucalyptus is added to the air. But how might the system work in natural life? With increasing distance from home, similarity of olfactory input with home site input should gradually decrease. From what dissimilarity onwards should the map system be activated? Is the activation also gradual? A little bit, more, full activation? How does a half-activated map work?

(6) If it is not the questionable and superfluous home versus nonhome message that causes navigationally irrelevant 'nonsense odours' to affect navigational output, what else makes odours such as eucalyptus helpful for homeward orientation by use of nonolfactory map cues? I do not find an answer in the JMP papers.

(7) What does the term 'activation' as used by JMP mean? Is it analogous to 'motivation'? Are pigeons not motivated to think about homing as long as they do not smell an unfamiliar odour, although they are informed about their position away from home and can, once flying, easily see that they are not above their loft area? Are definitely anosmic birds (e.g. by olfactory nerve section) motivated to fly long distances (>100 km straight line) in arbitrary directions (Figure 7.3 in W2005a; see also Gagliardo et al., 2013), but not motivated to direct their courses homeward by asking or activating their nonolfactory map which could tell them where to fly? Pigeons that could smell either release site air or (according to JMP) nonsense odours before release while sitting in a box, but then start flying in an anosmic state (nasal anaesthesia) depart in the direction of home. If we follow JMP, these birds are motivated to resurrect the navigational conclusions they had previously drawn in the box (groups FC and NV in JMP10 >2 h ago) from nonolfactory map cues, but are not motivated to use currently available nonolfactory cues, because currently they are unable to smell.

(8) If we accept that lack of olfactory input or lack of nonhome odours demotivates pigeons to return to their loft, we might expect that demotivation affects homing based on any kind of cues. Actually, according to JMP09, in addition to the use of undefined nonolfactory map cues, a very different mechanism, path integration, needs olfactory input as well. A third method of finding home, however, does not need olfaction: anosmic pigeons are well oriented towards home when released within a familiar area, even if they cannot follow an entrained sequence of landmarks from the