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The effect of age, sex and gonadectomy on dogs' use of spatial navigation strategies

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ABSTRACT

In this study we assessed the effect of sex and gonadectomy on the type of spatial strategy (allocentric or egocentric) preferentially used by dogs in the acquisition of a navigation task and their ability to resort to the non-preferred strategy. Fifty-six dogs were involved in the study, divided in four equally sized groups based on sex and gonadectomy. Dogs initially underwent a learning phase, where they entered a plus-shaped maze from one arm and had to learn the position of a food bowl, which was placed in one of the lateral arms. The task could be achieved by relying on an either egocentric (i.e. learning to turn left or right) or allocentric strategy (i.e. using the external cues provided within the maze as a reference the position of the baited bowl). Following training, dogs were let in the maze from the entrance opposite to the one used in the learning phase, so that use of an egocentric strategy would lead them to search for food in one arm, while using an allocentric strategy would lead them into the opposite arm. Dogs' choices were used to determine their preferred strategy. In the last training phase, we assessed dogs' ability to resort to their non-preferred strategy to find the baited food bowl, by removing external cues and placing the baited bowl always at the same side of the dog, for subjects deemed as allocentric, and by keeping external cues and placing the baited bowl in a constant location relative to the cues, for dogs deemed as egocentric. No effect of sex was found on strategy preference, but ovariectomized females were significantly more likely to prefer an egocentric strategy, implying a role of ovarian hormones in biasing navigation strategies. The probability of resorting to the non-preferred strategy increased with aging in females and decreased in males. The higher requirement to cope with unpredictable environments during dispersal may support a predisposition to flexibly use different sources of information in younger males. By contrast, experience may be needed by females to reach the same proficiency, thereby justifying the increase in flexibility with ageing. In addition to increasing our knowledge about navigation, these results highlight effects of sex and ovariectomy on dog cognition, with potentially important implications regarding the management of dogs in different fields.

1. Introduction

Spatial navigation entails cognitive processes that allow mobile animals to know where they are and to find a way back to their shelters, or to access resources, by using multiple cue sources, such as path integration, magnetic cues and different landmarks (Brodbeck and Tanninen, 2012). The spatial cognitive processing requires memorizing specific landmarks, positions and locations, allowing, in its most sophisticated form, to elaborate a cognitive map in order to orientate oneself and navigate in the surrounding environment.

In the last decades, a body of researches underlined sex differences in spatial navigation tasks in mammals with males showing generally better performances, possibly due to a different involvement in the reproductive function (Astur et al., 2004; Clint et al., 2012; Hawley et al., 2012; Healy et al., 2009; Shah et al., 2013). On the one hand, males' advantage in solving spatial navigation tasks could have been inherited from competition for mating, that in most cases encompasses an extended home range (Ecuyer-Dab and Robert, 2004; Macdonald and Carr, 1995; Pal et al., 1998) compared to females. Such sex differences are typical of polygynous, rather than monogamous species, underlining the link between reproductive strategies and spatial cognitive abilities (Ecuyer-Dab and Robert, 2004). On the other hand, females' higher involvement in protection of the offspring, may have favoured a superior spatial ability in spatially restricted areas, using

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memory of nearby spatial information (Ecuyer-Dab and Robert, 2004; Guillamón et al., 1986; Herman and Wallen, 2007). Different navigation strategies have also been highlighted, with males seemingly preferring an allocentric navigation – i.e. using the relative position of the objects inside the surrounding space to orientate – and females exhibiting a bias for egocentric navigation strategy, referring prevalently to their motor responses (Hawley et al., 2012; Herman and Wallen, 2007; Jonasson et al., 2004).

Sexual hormones are one of the physiological factors driving these sex differences in spatial navigation. Sexual hormones act at organizational level, shaping the brain during development (Isgor and Sengelaub, 1998; Williams et al., 1990), but they also have activational effects, leading to differences between sexes (or even within one sex, e.g. across the oestrous cycle) in adult individuals (Daniel, 2006; Martin et al., 2007). For instance, a detrimental effect of ovariectomy has been observed in the acquisition of radial arm maze (Daniel et al., 1999). Furthermore, castration adversely affects working memory (a limited capacity resource used for temporarily preserving information while simultaneously processing the same or other information) during navigation, but it does not significantly impair reference memory (a long-lasting memory used to store information that remains constant over time) in male rats (Gibbs and Johnson, 2008; Locklear and Kritzer, 2014). Ovariectomized female rats show worse navigation abilities, which encompass a decrease in both working and reference memories (Gibbs and Johnson, 2008), whereas oestrogen administration quickly improves spatial reference memory in reproductively quiescent female mice (Frick et al., 2002).

Dogs, as polygynous species with a different involvement in reproduction between sexes, are a good candidate to study sex differences in spatial navigation. Dogs showed a great ability to solve different spatial tasks, thanks to the use of a wide range of spatial skills. They have better memory for spatial locations presented before in a spatial list (primacy effect) rather than ones presented later (recency effect) (Craig et al., 2012). They are capable of integrating spatial signals during locomotion, continuously updating the information about the distance and direction from an object (path integration; Cattet and Etienne, 2004) and developing novel paths based on knowledge of paths already used before (Séguinot et al., 1998). In a landmark-based search paradigm, dogs proved to be able to encode spatial information related to local and global allocentric cues (Fiset 2009, 2007). They can use both egocentric and allocentric references in different type of tasks (Cattet and Etienne, 2004; Chapuis et al., 1983), showing to prefer egocentric strategy to solve an object finding task and to flexible switch to the non-preferred strategy when the preferred one became useless (Fiset et al., 2000; Fiset and Malenfant, 2013). In a social learning paradigm, we recently showed that dogs preferentially relied on allocentric information in matching the location of the owner's demonstration (Fugazza et al., 2017). On the other hand, dogs were able to learn an egocentric strategy when allocentric cues were made unreliable, with males more skilful than females.

Maze paradigms represent a valid tool in canine models to study the functions involved in spatial navigation (Craig et al., 2012; Macpherson and Roberts, 2010; Mongillo et al., 2015, 2013; Parson et al., 2016) and the plus-maze has been proved one of the most effective type to assess navigation strategies both in humans and laboratory animals (Harris et al., 2012; Packard, 2009). A previous study performed by our research group demonstrated the feasibility of a T-maze paradigm to study spatial learning, long term memory and reversal learning (i.e. flexibility), showing an impairment in reversal learning abilities in older dogs (Mongillo et al., 2013). We also showed that female dogs were faster than males in acquiring a spatial learning task, but no difference emerged between sexes in the reversal learning task (Mongillo et al., 2017). However, gonadectomy affected spatial learning in females, with ovariectomized females performing significantly worse than intact subjects, whereas no effect was found for the orchiectomy in male dogs (Mongillo et al., 2017). While these studies underline the importance of sexual hormones in driving spatial cognitive bias, they also point out the importance of studies aimed to disentangle the effect of gonadectomy on cognitive skills. One of many questions to be answered is how sex and gonadectomy affect spatial navigation and memory in dogs. The inclusion of gonadectomized subjects, will help towards a better understanding of the mechanisms underpinning sex differences at functional level, and shedding more light on the effect of this common surgical practice on the dog's cognitive skills.

To the best of our knowledge, there are no studies investigating the effect of the gonadectomy in the use of egocentric or allocentric strategies during spatial navigation in dogs. Thus, the aim of this research was projected to evaluate the effect of the sex and gonadectomy on the type of strategy preferentially used by dogs in the resolution of spatial navigation tasks. Specifically, we first assessed whether dogs would preferentially use allocentric or egocentric reference frame in acquiring the plus maze paradigm. Subsequently, we assessed dogs' ability to resort to their non-preferred strategy, when such strategy becomes inadequate to solve the task. In view of previous literature pointing to a prominent role of ovarian hormones in influencing spatial cognition, we expect to find the largest differences between intact and ovariectomized females in the use of spatial strategies. In addition, based on our own findings – although produced in substantially different tasks – we may expect females to outperform males in the initial acquisition tasks, but males to outperform females in the acquisition of the non-preferred strategy task.

2. Materials and methods

2.1. Subjects

Fifty-six healthy pet dogs were recruited through advertisements in veterinary clinics, parks, and the University of Padua. Recruitment criteria included age between two and eight years, and high motivation for food, which was assessed by the experimenter by presenting the dogs a piece of sausage, just prior to the beginning of the experimental procedures. In addition, sex and gonadectomy were taken into account for recruitment so that four groups of the same size (N = 14) were formed, including intact (non-orchiectomized) males (IM, mean age ± SD: 4.4 ± 2.4 years), orchiectomized males (OM, 4.4 ± 1.2 years, orchiectomized at 18.0 ± 14.2 months of age), intact (non-ovariectomized) females (IF, 3.4 ± 1.5 years) and ovariectomized females (OF, 4.0 ± 1.9 years, ovariectomized at 17.2 ± 12.8 months of age) of different breeds were formed.

Experimental groups did not significantly differ for the mean age ($F = 0.94$; $P = .43$); there was no difference in age at gonadectomy between gonadectomized males and females ($t = 0.15$, $P = .88$).

All tests were conducted at the Laboratory of Applied Ethology (Department of Comparative Biomedicine and Food Science, University of Padua) in a room of about 5 × 5 m.

2.2. Assessment of preferred strategy

This procedure was meant to determine for each dog the preferred strategy in the acquisition of a simple navigation task. The procedure included a learning phase, where dogs had to learn the position of a food bowl within a plus maze, followed by a strategy assessment trial, where egocentric and allocentric frames of reference were put in contrast, allowing to point out each dog preferred strategy. The learning phase and the subsequent assessment test were administered twice or three times as detailed below, to determine the consistency of dogs' preferred strategy and classify dogs as preferentially 'egocentric' or 'allocentric'.

2.2.1. Experimental setting

In this part of the procedure, we used a plus-shaped maze (Fig. 1). The maze was made of plastic panels with a height of 2.0 m. Two of the