Neuroscience and Biobehavioral Reviews 72 (2017) 232–242

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

Review article

Mate-choice copying, social information processing, and the roles of oxytocin

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ARTICLE INFO

Article history:
Received 4 October 2016
Received in revised form
23 November 2016
Accepted 1 December 2016
Available online 5 December 2016

Keywords:
Social recognition
Social learning
Sexual behavior
Social odors
Mate preference

ABSTRACT

Social and sexual behaviors, including that of mate choice, are dependent on social information. Mate choice can be modified by prior and ongoing social factors and experience. The mate choice decisions of one individual can be influenced by either the actual or potential mate choice of another female or male. Such non-independent mate choice, where individuals gain social information and socially learn about and recognizes potential mates by observing the choices of another female or male, has been termed "mate-choice copying". Here we first briefly review how, why, and under what circumstances individuals engage in mate-choice copying. Secondly, we review the neurobiological mechanisms underlying mate-choice copying. In particular, we consider the roles of the nonapeptide, oxytocin, in the processing of social information and the expression of mate-choice copying.

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1. Introduction

Animals need and seek information to make adaptive decisions – for example what to eat, who to interact with or avoid and who to mate with. The better informed an individual is the better it can deal with its' physical and social environment (Danchin et al., 2004; Dall et al., 2005; Seyfarth et al., 2010; Valone and Templeton, 2002). Social information arises either as direct signals from others and, or indirectly (inadvertently, public information) as cues or by-products produced by the behavior and decisions of others with similar needs and requirements. Individuals pay attention to what others are doing (e.g. what they are eating) and in general whom (e.g. potential mates) and what they are either interested in or avoiding (e.g. Choleris et al., 1997, 2009; Clipperton

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http://dx.doi.org/10.1016/j.neubiorev.2016.12.003
0149-7634/

et al., 2008; Dugatkin, 1992; Galef, 1988; Galef and White, 1988. Kavaliers et al., 2005, 2006).

Social information use involves social cognition and the acquisition and cognitive processing of information about others (i.e. social recognition) as well as information originating from others (i.e. social learning), accompanied by the exploitation and application of that information in subsequent decision making (Choleris et al., 2009).

Social recognition in its' broadest is the ability of an animal to distinguish conspecifics including potential social and sexual partners and competitors based on either innate responses to, or past experiences with others. Social recognition and discrimination involves multi-modal signal and cue recognition at various levels during social interactions or observations. This includes; sex, reproductive status (e.g. estrous phase, testosterone levels), condition and quality (e.g. parasite load and infection status), diet, microbiome composition, immune and stress condition, social hierarchy (e.g. dominant, subordinate, level of aggression), genetic relatedness, familiarity and true individual recognition (see Archie and Tung, 2015; Baum and Kelliher, 2009; Brennan and Kendrick, 2006; Choleris et al., 2009; Johnston, 2003; Kavaliers et al., 2003, 2004, 2006; Lai et al., 2005; Mateo, 2004). Social recognition incorporates rapid and flexible learning and memory to deal with the changeable social environment and social information available.

Social learning can be defined as when "learning is influenced by observation of, or interaction with, another animal or its products" (Box, 1984; Galef, 1988; Heyes, 1994). Social learning allows an individual to circumvent the disadvantages and risks associated with individual learning by "exploiting the expertise of others" (Russon, 1997). Social learning has been shown to be used in situations ranging from where and what to eat (learning of food locations and preferences), avoidance of aversive situations (e.g. fear learning and avoiding predators, threatening conspecifics) to the recognition and choice of potential mates ("mate-choice copying") (e.g. Choleris et al., 1997, 2009; Clipperton et al., 2008; Dugatkin, 1992, 1996; Griffin, 2004; Galef, 1988; Galef and White, 1988; Kavaliers et al., 2005, 2006; Little et al., 2011a,b; Vakirtzis, 2011; White, 2004). Social recognition also has an important role in the expression of social learning. For example in the social learning of fear by deer mice observers learn better from dominant than subordinant demonstrators, while in the social learning of food preferences gerbils learn from familiar individuals and kin but not from unfamiliar individuals (Kavalierset al., 2005; Valsecchi et al., 1996).

Social cognition involves not only successfully assessing other individuals and their behavior but also deciding whether and how to interact with them and utilize the social information they provide. Animals adjust their use of social information according to the reliability of the information content, costs, and their own experience (Bonnie and Earley, 2007; Westneat et al., 2000). This adaptive use of social information is particularly relevant in the context of mate choice and utilizing the mate choice decisions of others (i.e. mate-choice copying) which is the focus of the present review.

1.1. Mate-choice copying and social cognition

Mate choice has been described as a social cognitive process that involves: (i) perceiving and receiving sexual signals and cues that provide information about potential mates; (ii) integration and processing of the sensory inputs providing information about potential mates; and (iii) searching for and discriminating between individuals; and (iv) deciding to mate with specific individuals (Jennions and Petrie, 1997; Cummings and Ramsey, 2015). Mate choice incorporates both preference (i.e. order in which an individual ranks potential mates) and choosiness (i.e. responsiveness to and discrimination between potential mates) (Brooks and Endler, 2001; Edwards, 2015; Jennions and Petrie, 1997). It is also now accepted that learning, and in particular social learning, plays an important role in determining mate choice (Miller and Todd, 1998; Verzijden et al., 2012). There is ample evidence from multiple species that the mate choice decisions of one individual can be influenced by either the actual or potential mate choice of another. Such non-independent mate choice where individuals gain information and socially learn about potential mates by observing conspecifics has been termed "mate-choice copying".

There is growing evidence that mate-choice copying is an integral component of human mate choice. Humans pay attention to and are influenced by the social and sexual preferences and choices of others (Jones et al., 2007; Little et al., 2011a,b). As such it is important to understand the underlying behavioral and neurobiological mechanisms associated with mate-choice copying. Although in both human and non-human mate-choice copying involves basic components of social learning and social recognition mate-choice copying has received scant attention in the neuroscience literature. Ecological and ethological investigations of mate-choice copying have focused on questions of: (i) who to copy (or who to reject); (ii) what signals or cues to use; (iii) when and where (i.e. under what conditions, context) to engage in mate choice copying. In marked contrast, the neurobiological basis of mate choice copying has until relatively recently received little attention (Choleris et al., 2009; Kavaliers et al., 2006). This is surprising as there has been concerted interest in, and investigations of, the neurobiological mechanisms associated with social recognition and social learning, the two major underpinnings of mate choice copying (e.g. Choleris et al., 2009; Ervin et al., 2015a,b). Here we: (i) briefly discuss selective aspects of who, what, when and where to copy and how they relate to social learning and social recognition and; (ii) review initial investigations of the neurobiological mechanisms associated with mate choice copying and, in particular, the roles of the nonapeptide, oxytocin.

2. Who, what, when and where to copy

2.1. Basics of female mate- choice copying

Mate-choice copying was originally investigated with females, whereby the mate choice of a particular male by one female causes an increased preference for the same male by another female (Dugatkin, 1992, 1996). Thus, when a female (the observer or copier) observes another female (the demonstrator or model) paired with a male (target) she subsequently remembers and prefers that male target when given a choice between two males (Fig. 1A). Mate choice copying entails using and processing social information from others (ie. social learning from the demonstrator) as well as social information about others (i.e. social recognition of target and model). Copying incorporates the emotional and motivational components of mate-choice and their influences on cognition. This likely involves the enhancement of a generalized arousal that facilitates sexual motivation (Ågmo, 2011; Quinkert et al., 2011; Weil et al., 2010). Thus, mate-choice copying may allows for an augmented arousal in the observer leading to an enhancement of the salience of the choices made and sensory cues used by the demonstrator.

As such mate choice copying can impact both preference and choosiness, affecting both the responsiveness to, and discrimination of, potential mates. Social learning of mate choice drives social recognition and subsequent social preferences. Individuals can potentially benefit from mate-choice copying through a reduction of the uncertainty of mate assessment, improvement in the discrimination of potential mates, and a reduction in the associated costs and risks (Blanchet et al., 2010; Bonnie and Earley, 2007; Dall