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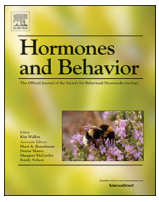

Review article

The challenge hypothesis revisited: Focus on reproductive experience and neural mechanisms

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ABSTRACT

Our review focuses on findings from mammals as part of a Special Issue "30th Anniversary of the Challenge Hypothesis". Here we put forth an integration of the mechanisms through which testosterone controls territorial behavior and consider how reproductive experience may alter these mechanisms. The emphasis is placed on the function of socially induced increases in testosterone (T) pulses, which occur in response to social interactions, as elegantly developed by Wingfield and colleagues. We focus on findings from the monogamous California mouse, as data from this species shows that reproductive status is a key factor influencing social interactions, site fidelity, and vigilance for offspring defense. Specifically, we examine differences in T pulses in sexually naïve versus sexually experienced pair bonded males. Testosterone pulses influence processes such as social decision making, the winner-challenge effect, and location preferences through rewarding effects of T. We also consider how social and predatory vigilance contribute to T pulses and how these interactions contribute to a territory centered around maximizing reproduction. Possible underlying mechanisms for these effects include the nucleus accumbens (rewarding effects of testosterone), hippocampus (spatial memories for territories), and the bed nucleus of the stria terminalis (social vigilance). The development of the challenge effect has provided an ideal framework for understanding the complex network of behavioral, environmental, physiological and neural mechanisms that ultimately relates to competition and territoriality across taxa. The opportunity to merge research on the challenge effect using both laboratory and field research to understand social behavior is unparalleled.

1. Introduction

The challenge hypothesis altered the perspective of how hormones function by illustrating how androgen levels in males fluctuate in response to the surrounding challenges from competitors. This creative perspective was pioneered by Wingfield et al. (1990) and developed primarily on data from birds. These ideas were rapidly applied to other taxa (reviews by Fuxjager et al. (2017), Hau et al. (2008), Hirschenhauser and Oliveira, 2006, and Tibbetts and Crocker (2014). An important feature of this hypothesis was the idea that social interactions can induce rapid but transient increases in testosterone (T), which we refer to as a T pulse. These T pulses are typically induced by social experiences such as aggressive encounters or mating opportunities. They can also be induced experimentally, typically through the use of water soluble, cyclodextrin-conjugated T solutions. Variability in the timing and duration of T pulses has been identified across taxa (review by Marler et al. 2005; Moore et al., 2019: this issue; Wingfield, 2019: this issue), and illustrates how plastic this mechanism can be in response to varying selection pressures. The classic example for a timed increase in T was found in resident song sparrows in the field at 10 min after a male intrusion (Wingfield and Wada, 1989). In California mice and other rodents T pulses can be delayed and occur ~15–45 min after competitive encounters (Sachser and Prove, 1984; Scotti et al., 2009), with individual variation in expression of the T increase. A virtually identical delayed T pulse can also occur after male-female encounters (Amstislavskaya and Popova, 2004) (Zhao and Marler, unpublished data). Research with California mice has focused on the functions of these rapid and transient T pulses before, during, or after an encounter (see Fuxjager et al., 2017). The goal of the current review is to expand on the relationship with timing of the behavioral changes and the T pulses with a focus on mammals, and also put it in the framework of both initiating and maintaining territoriality. The most well developed mammalian models for the challenge effect are the California mouse (*Peromyscus californicus*) and humans. Here we focus on the rodent

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literature as the challenge effect in humans has been reviewed elsewhere (Fuxjager et al., 2017; Gray et al., 2019: this issue).

In California mice, we have a model system in which we can tightly control environmental and neuroendocrine variables to address mechanistic underpinnings of the challenge effect. The highly monogamous California mouse is biparental, territorial and expresses lifelong pair bonds (e.g. Gubernick and Alberts, 1987; Gubernick and Teferi, 2000; Gubernick and Nordby, 1993; Marler et al., 2008; Ribble, 1991; Ribble and Salvioni, 1990). Male California mice establish territories relatively close to their natal territory and attract a female that has typically moved a greater distance from her natal territory (Ribble, 1991, Ribble, 1992a, b). Courtship, as assessed from laboratory studies, includes at least following behavior and the production of ultrasonic vocalizations (Gleason and Marler, 2010; Pultorak et al., 2015; Pultorak et al., 2018). Pair bond formation involves a series of behavioral and hormonal changes (Becker et al., 2012; Pultorak et al., 2015, 2018; Zhao and Marler, 2014; Zhao and Marler, 2016) and coincides with the pair defending an exclusive territory against both male and female intruders with high levels of aggression (field: Ribble, 1992a, b; lab: Davis and Marler, 2003; Oyegbile and Marler, 2005; Fuxjager et al., 2017; Rieger and Marler, 2018; Rieger et al., 2019). Among mammals, including *Peromyscus* species, infanticide occurs and may be a driving force for territorial behavior by both males and females (Agrell et al., 1998; Alexander et al., 1994).

Our goals are to examine the relationship between testosterone pulses and behavior within the framework of territoriality in a mammal by (1) reviewing both rapid and long-term responses to T pulses related to immediate social decision making and future ability to win male-male encounters, (2) discussing research linking T pulses and location preferences (conditioned place preferences; CPPs) and (3) consider how social vigilance both before and after encounters may control the timing of T pulses and impact their function. We further (4) explore the neural substrates that may underlie territoriality including the hippocampus as related to spatial information, reward brain areas such as the nucleus accumbens as related to reward-driven behavior, and the bed nucleus of the stria terminalis (BNST) as related to vigilance.

2. Effects of T pulses on behavior

2.1. Rapid and long-term effects of T pulses on social behavior, mechanisms for social competition

When initiating territoriality, a male must assess both the physical resources available and the surrounding social environment. A sexually naïve male California mouse needs to negotiate the demands for courting a female and also for repelling other males from his exclusive territory, as is characteristic of California mice (Ribble, 1992a, 1992b). Do testosterone pulses during social interactions influence approach to unfamiliar males or females? This was tested by Zhao et al. (2019) with the additional question of whether past social experience can alter the effect of T pulses after males have become bonded? A paired or unpaired (sexually naïve) male was administered a T pulse, and the immediate effects on choosing to approach an unfamiliar male or female (both sexually naïve) in a two-choice test was examined. In unpaired males, a T pulse shifted behavior from a greater tendency to approach an unfamiliar female over a male towards a bias for approaching an unfamiliar male. In contrast, T pulses had no effect in paired males. These results reveal that T pulses can immediately influence social decision making and that effects can vary based on past sexual experience/pair bonding status (as suggested by Bell, 2019: this issue). In unpaired males that are initiating territoriality, the T pulse may therefore increase the social decision to approach and potentially expel males from the territory, as might occur in a wide variety of territorial species. Interestingly, the study also showed that within the sexually inexperienced males, some males preferentially approached males and others preferentially approached females. Males that preferentially approached females exhibited higher levels of aggression in male-male encounters. This is consistent with the idea that personality or behavioral types are important considerations when studying the challenge effects within a species (Bell, 2019: this issue).

We can also ask whether the T pulses experienced after an aggressive encounter can influence future aggression? Previous work has shown that individuals that win aggressive encounters are more likely to win in the future (winner effect; Fuxjager et al., 2009, Fuxjager and Marler, 2010; Oyegbile and Marler, 2005; Trainor et al., 2004; Trainor and Marler, 2001), but did not focus on underlying mechanisms. According to the winner-challenge hypothesis, T pulses after an encounter provide a mechanism to amplify ability to win (Oyegbile and Marler, 2005). Can multiple T pulses and/or multiple winning experiences result in a cumulative effect that might represent a sampling of the social environment? This integration would be valuable for establishing and maintaining a territory through the ability to compete but avoid the costs of heightened territoriality in the absence of social competition. The strongest support is found in a series of studies mimicking the natural T pulse at 45 min after a male-male encounter and examining the effect on winning behavior in response to a number of manipulations (Fuxjager et al., 2009, Fuxjager and Marler, 2010; Oyegbile and Marler, 2005; Trainor et al., 2004; Trainor and Marler, 2001). Both the winning experience and the T pulses are required to develop a full winner effect in the future (Fuxjager et al., 2011). The release of this T pulse is plastic such that if the winning experience takes place in an unfamiliar environment, no T pulse occurs (Fuxjager and Marler, 2010). This is similar to male athletes that experience a T pulse after winning at a “home game” but not at an “away game” (Carré, 2009; Casto and Edwards, 2016). The post-encounter T pulse then is only one of potentially many contributing factors to the development of the winner effect which include the winning experience, the location during training (past experience) and the location of the final encounter (Fuxjager et al., 2009, 2011; Fuxjager and Marler, 2010). The essential nature of the T pulse for some behaviors was, however, revealed when post-encounter T pulses were administered to the promiscuous white-footed mouse, which lacks a post-encounter T pulse and a winner effect; the result was a dramatic development of the winner effect (Fuxjager et al., 2011). When a given study does not find the challenge effect present in a species, it cannot be ruled out that it might be expressed under different conditions, or that it would be detected using a different timeline because of the frequently transient nature of the challenge effect. For example, it is possible that white-footed mice might display a challenge effect under different conditions such as the inclusion of the presence of a female, as suggested by Moore et al. (2019: this issue).

Within this series of studies, it was further found that the T pulse itself is acting through androgen receptors to influence experience induced increases in ability to win, as aromatase inhibitors (which block conversion of T to estradiol) do not block the effects of T pulses (Trainor et al., 2004). In contrast, dopamine receptor antagonists administered after winning experiences (in mice exhibiting endogenous T pulses) effectively block winner effects (Becker and Marler, 2015). The involvement of dopamine signaling raises the possibility of reward-based mechanisms to be involved in the winner-challenge effect, as described below.

2.2. T-induced location preferences (conditioned place preferences; CPPs), a mechanism for territoriality

In the context of the challenge effect, one function of T pulses that has been overlooked is whether T pulses are perceived as rewarding. T pulses induce conditioned place preferences in California mice (Zhao and Marler, 2014) and other rodents (Alexander et al., 1994; Arnedo et al., 2000; Frye et al., 2001; Packard et al., 1997; Rosellini et al., 2001; Sato et al., 2010). This classic behavioral test provides insights into whether a hormone or drug is perceived as rewarding. Again, however, we find plasticity in the effects of T pulses related to both

social experience and the location of the experience. Pair bonding can diminish the rewarding effects of T (Zhao and Marler, 2014). Critically, however, for both paired and unpaired males the location in which a male is conditioned effectively alters the conditioning properties of T pulses. The typical design for a conditioned place preference in a three chambered CPP apparatus is for the middle chamber to be neutral, however, (Zhao and Marler, 2014; Zhao and Marler, 2016) modified this so that the middle chamber served as home chamber, which is more similar to what might occur in the field. First, the two side chambers were closed off while the home site was established in the middle chamber. During this time, paired males were housed with a pair-bonded female in the middle chamber, whereas unpaired males were housed with their same sex cagemates. Unpaired, sexually naïve males could be T-conditioned to an unfamiliar location (side chamber) but not the central home chamber, possibly because it was too similar to the natal territory. In contrast, paired males were T-conditioned to the central chamber where the mate was previously located, but not the unfamiliar side chambers. The salient location for an unpaired male may be an unfamiliar location in which the male could establish a new territory, whereas the salient location for a paired male may be his home territory where he has formed a bond with his mate (review by Rieger et al., 2018). The T-induced CPP may therefore be used for initiating territoriality and/or adjusting time allocation towards specific locations in a territory. Unpublished data indicate that T also induces changes in time allocation to specific locations as well such as time spent at the nest (Petric, Kalcounis-Rueppell and Marler, unpublished data). How does this interact with aggression? Additional unpublished data suggest that the formation of a T-induced CPP does not amplify aggressive motivation to approach another male above and beyond that of the effect of T on aggressive motivation to approach a male in the absence of the formation of a CPP (Zhao et al., 2019). This is consistent with data from mice showing that neural mechanisms modulating the intensity of aggression can be dissociated from pathways modulating the rewarding aspects of engaging in aggression. It should be noted that rats and Syrian hamsters will voluntarily self-administer T (Wood, 2002; Wood et al., 2004), which reinforces the idea that T pulses are perceived as rewarding. The primary take home message for this section is that not only can T pulses induce CPPs, but that this effect is context- and experience-dependent. The induction of place preferences by T pulses could play a key role in the formation of new territories in virgin males and the maintenance of existing ones in paired males.

Thus far, we have critical components that link territoriality with T pulses and the potential behaviors that may help to carve out a territory in a competitive social environment. A potential scenario is that T pulses increase the probability that a sexually naïve male will approach a male instead of a female, which may be an initial step contributing to a tendency to compete with other males. The T pulses can then further amplify a winner effect and associated aggression in an area being assessed as a likely home site. This also contributes to competition with other males. Finally, the T pulses may help form a preference for a location suitable for a territory and/or modify time allocation within that territory (reviewed in Rieger et al., 2018). Testosterone may also act on other behavioral processes that play a key role in territory formation. In the next section we consider the role of social vigilance in territory formation and how T pulses may modulate this behavior.

2.3. Social vigilance, a mechanism for deciding to engage

As reviewed above, T plays a key role in shaping when and where aggressive behaviors occur. Less is known about how individuals make the transition from a less competitive juvenile to becoming a more competitive adult that can win aggressive contests. A potentially important behavioral mechanism is social vigilance, during which individuals monitor social contexts. Work in fish (Burmeister et al., 2005; Maruska and Fernald, 2010) and mice (Curley, 2016; Williamson et al., 2019) shows that removal of a dominant male results in increased aggression of less dominant males within minutes. These rapid behavioral and corresponding neuroendocrine transitions show that lower-status individuals are attuned to the social environment. Social vigilance may thus be an important mechanism that leads to winning experiences. Prior to winning experiences, social vigilance is primarily observed in combination with social avoidance. After winning experiences, social vigilance behavior may take different forms such as protecting offspring or monitoring for potential competitors. Testosterone could play a key role in this transition.

Social vigilance can be quantified in several ways. In a laboratory setting, the amount of time an animal spends oriented towards an unfamiliar individual is increased after unsuccessful competitive encounters (Duque-Wilckens et al., 2018; Williams et al., 2018). Interestingly, individuals with low social status often reduce feeding behavior to engage in visual scanning (Blumstein et al., 2001; Ekman, 1987; Shepherd et al., 2006), which is also an important form of anti-predator behavior. One version of scanning behavior is the “stretch-attend” posture, which consists of orienting towards a threat while maintaining a crouched posture that reduces visibility. Stretch-attend postures are evoked by social threats (Hubbard et al., 2004), suggesting possible convergent mechanisms with anti-predator behaviors.

In California mice, social vigilance has been studied primarily in the context of losing social encounters (Steinman et al., 2019). In adults, losing social encounters has stronger long-term effects on social vigilance in females than males. Two weeks after losing experiences, females but not males exhibit avoidance and vigilance towards unfamiliar mice (Duque-Wilckens et al., 2018; Williams et al., 2018). Although this sex difference was still observed in gonadectomized individuals (Trainor et al., 2013), social vigilance may still be sensitive to gonadal hormones. When losing experiences occur before puberty, both males and females respond to unfamiliar mice with avoidance and vigilance (Wright and Trainor, in preparation). This suggests that gonadal hormones can shape social vigilance, with the temporary increase in baseline T during puberty most likely inhibiting the development of prolonged stress-induced vigilance. In contrast, T pulses in adults might have very different effects on vigilance compared to developmental effects of baseline T levels.

Studies examining vigilance in the context of parental behavior support this idea. In addition to provisioning and caring for offspring, protection from predators or competitors is a fundamental aspect of parental care in many species (Bosch, 2013; Gammie, 2005). In males, parental aggression could have important links with T. These potential links have been understudied, perhaps because in most male mammals, T levels are lower following the birth of offspring (Gleason and Marler, 2010; Reburn and Wynne-Edwards, 1999; Storey et al., 2000; Trainor et al., 2003; Ziegler, 2000). However, research in humans suggests that the impact of T pulses in response to infant stimuli could be underappreciated. Specifically, infant cries can generate rapid increases in T in fathers (Storey et al., 2000) (Fleming et al., 2002) and T administration enhances neural responses to infant cries in women (Bos et al., 2010). These rapid increases in T are context dependent, and are primarily observed when infant cries are heard but there is no opportunity to directly interact with the infant. One possible explanation for this T pulse is that it may play a role in infant defense (van Anders et al., 2011) as found in aggressive offspring defense in both blue-gill sunfish and small mouth bass with sole paternal care (Rodgers et al., 2012; O'Connor et al., 2011). If so, increased T might enhance vigilance for potential threats. If threats are predictable, there is evidence for T to have a preparatory or anticipatory function, at least in the context of sports in humans (review by Fuxjager et al., 2017). For rodents, apart from predators, there is likely a strong selection pressure to address infanticidal behavior by conspecifics (Agrell et al., 1998).

From an adaptive behavioral perspective, the multiple effects of T on territorial behavior merge into a suite of traits that allow for territorial fidelity, vigilance for evicting intruders, and social decision making (Fuxjager et al., 2017). Many of these effects appear to be

influenced by T pulses, but basal levels of T may contribute as well and need to be explored, especially in the context of vigilance.

(4) Androgen-sensitive neural substrates underlying territorial behavior

We explore a subset of brain areas that may contribute to different aspects of territory formation and maintenance including the nucleus accumbens, hippocampus and bed nucleus of the stria terminalis. A number of other brain regions express androgen receptors and are associated with aggression are not included in this review such as the medial amygdala (Clinard et al., 2016) and ventromedial hypothalamus (Falkner et al., 2016). Most work on amygdala and hypothalamic modulation of aggression focuses primarily on intensity of aggression rather than other aspects of territoriality (Kruk et al., 1998; Yamaguchi and Lin, 2018). Below we highlight specific brain regions that link rewarding aspects of T, association of T with site fidelity and the vigilance needed to protect offspring and the territory.

3. Brain regions linking rewarding aspects of T, association of T with site fidelity and the vigilance

3.1. Nucleus accumbens

Studies in mice have outlined how the nucleus accumbens (NAc) modulates aggression. Inhibition of both D1- and D2-family of receptors in the NAc reduce motivation to engage in aggression (as measured via lever pressing) but had weaker effects on specific aggressive behaviors like biting or chasing (Couppis and Kennedy, 2008). Reinforcing social experiences such as sexual behavior (Hedges et al., 2009; Pitchers et al., 2010) or winning aggressive encounters (Aleyasin et al., 2018) leads to increased expression of ΔFosB in the NAc. In female California mice, a same sex aggressive encounter increases c-fos in the NAc but only during estrus (Davis and Marler, 2004). Unlike other transcription factors such as c-fos, ΔFosB has a very long half-life and can thus accumulate over time (Robison and Nestler, 2011). Interestingly, ΔFosB has different effects on behavior through its actions in D1 or D2 receptor expressing neurons. Overexpression of ΔFosB in NAc D1 neurons enhanced aggression intensity in males while overexpression of ΔFosB in D2 neurons enhanced the formation of CPPs to locations where the male defeated an intruder (Aleyasin et al., 2018). Neurons expressing D1 receptors in the NAc shell also control motivation to engage in aggression (Golden et al., 2019). Together these results suggest that D1 expressing neurons in the NAc may be more important for motivation to engage in aggression while D2 expression neurons may play a more important role for generating the rewarding properties of winning aggressive encounters. A single-cell RNA-Seq study showed that androgen receptors are exclusively expressed in D1 and D2 medium spiny neurons and not in glial cells or cholinergic interneurons (Gokce et al., 2016). This suggests that both D1 and D2 pathways are directly activated by T surges. Consistent with these findings, T induces c-fos induction in the NAc (DiMeo and Wood, 2006) while infusions of water-soluble T (via cyclodextrin conjugation) into the NAc induce place preference formation (Packard et al., 1997). These pathways can be strengthened through experience, as California mice that won aggressive encounters in their familiar home cage had elevated androgen receptor expression in the NAc compared to controls (Fuxjager et al., 2010).

3.2. Hippocampus

T pulses could influence the formation of place preferences by altering hippocampal function. Several studies indicate that androgens can promote spatial memory formation (Benice and Raber, 2009; McConnell et al., 2012; Wagner et al., 2018), but most have applied long-term manipulations through gonadectomy or implants. However, T can act rapidly to increase spine density in hippocampal CA1 neurons (Hatanaka et al., 2015; Murakami et al., 2018), which are important for the formation and retrieval of spatial memories. This suggests the possibility that T pulses could modulate spatial memory formation. T pulses might also affect hippocampus-dependent social memories.

The mechanisms underlying social memories have been primarily studied using relatively simple social recognition tasks. Challenge effects are not necessarily based on social recognition of competitors, but a change in aggression based on experience is arguably a form of social memory. Thus, a consideration of neuroendocrine mechanisms of social recognition could be informative of pathways that could modulate challenge effects. In female rodents, social recognition is modulated by estrogens (Choleris et al., 2018; Ervin et al., 2013). Selective deletion of estrogen receptor α (ERα) reduce performance in social recognition tasks (Choleris et al., 2006, 2003; Imwalle et al., 2002), while ERα-selective agonists enhanced social recognition within 40 min of administration (Phan et al., 2011). Such rapid behavioral effects are usually assumed to be mediated by nongenomic actions of estrogen receptors (Laredo et al., 2014). The long-term effects of T surges after an encounter almost certainly involve non-genomic mechanisms because T levels are usually elevated for an hour or less (Marler et al., 2005).

One possible mechanism is through the action of vasopressin receptors, as T can induce vasopressin release (Crofton et al., 1985). In males, activation of vasopressin neurons projecting to the CA2 region of the dorsal hippocampus also prolonged social recognition for up to 1 week, an effect that is mediated by vasopressin V1b receptors (Smith et al., 2016). Other studies report that activation of CA2 hippocampal neurons projecting to the lateral septum facilitate aggression in a resident-intruder test (Leroy et al., 2018). Neurons within the ventral CA1 region of the hippocampus have also been found to play an important role in the formation of social memories (Okuyama et al., 2016). In this study, there was no quantification of aggressive behaviors, but these CA1 neurons were found to project directly to the nucleus accumbens shell. This suggests that these neurons could play a role in experience-dependent modulation of motivation to engage in aggression. A major weakness of rodent studies using modern neuroscience approaches is that most studies use simplified approaches to quantifying behavior that often lack ethological validity. Thus, while neural circuits modulating various aspects of social recognition or aggression have been identified under highly controlled conditions, it is unclear whether these mechanisms would generalize to more naturalistic contexts or situations.

3.3. Bed nucleus of the stria terminalis (BNST)

The BNST plays a major role in the control of social behavior (Bosch et al., 2010; Dumais et al., 2016; Jasnow et al., 2004; Masugi-Tokita et al., 2016), in part through its connections with other hypothalamic and limbic nuclei that modulate social interactions (O'Connell and Hoffman 2011). In addition, strong connections with the amygdala allow the BNST to play a key role in modulating behavioral responses to threats (Calhoon and Tye, 2015; Shackman and Fox, 2016). For example, predator odors induce robust activation of the BNST in rats (Day et al., 2004; Dielenberg et al., 2001) and mice (Janitzky et al., 2015) while selective inactivation of the anterior BNST reduces the expression of predator-induced defensive behaviors (Fendt et al., 2003). Although the BNST has long been known to be a key node in circuits of defensive behaviors, its role in social vigilance has only recently been explored. Studies in California mice show that the BNST plays a key role in modulating social vigilance, and that oxytocin is a key modulator of this behavior.

Activation of oxytocin receptors within the BNST results in avoidance of unfamiliar individuals as well as social vigilance (Duque-Wilckens et al., 2018). This orienting behavior does not occur in non-social contexts, suggesting that oxytocin enhances the salience of social contexts (Shamay-Tsoory and Abu-Akel, 2016). An untested idea is

whether oxytocin has a role for enhancing the salience of winning experiences. If so, such an effect may be more likely to occur outside of the BNST, as accumulating evidence suggest that different context-dependent effects of oxytocin on behavior are mediated by different neural circuits (Steinman et al., 2019). For example, for social interactions that are rewarding, oxytocin acting in the mesolimbic dopamine system plays a key role in the formation of place preferences (Dölen et al., 2013; Song et al., 2016). Current evidence suggests that the BNST is more important for conferring salience in aversive contexts.

The BNST expresses both androgen and estrogen receptors (Bamshad et al., 1993; Gegenhuber and Tollkuhn, 2019; Juntti et al., 2010), yet sex differences in the behavioral effects of losing encounters are not affected by gonadectomy in adult males or females (Trainor et al., 2013). However, since losing aggressive encounters leads to the expression of social vigilance in prepubertal males and females (Wright and Trainor in preparation), this suggests that gonadal hormones such as T may reprogram the BNST during adolescence. Although some nuclei undergo dramatic morphological and functional changes during puberty (Juraska et al., 2013; Piekarski et al., 2017), the BNST has not yet been studied at this timepoint.

4. Summary and future directions

Field studies, particularly with birds, have provided a wealth of data that provide information about when T pulses occur in response to changing social conditions, including variation across species. Research with humans highlights the broad applicability of the challenge hypothesis and provides insight into psychological components of the winner effect. Here we focused primarily on rodents, particularly the California mouse, which has allowed us to begin elucidating the -underlying mechanisms that mediate the actions of T pulses and challenge effects. We showed that T pulses characteristic of the challenge effect rapidly alter the decision to engage in aggression, most likely through non-genomic mechanisms. In addition to these short-term effects, T pulses contribute to the winner-challenge effect through longer term effects, such as enhancing location fidelity through rewarding effects of T. We also discussed social and predatory vigilance as a mechanism for deciding when to engage in encounters, and to potentially explain why parental behavior and aggression are positively associated in many mammals (instead of negatively associated in many species of birds). These behaviors can be broadly related to territoriality from winning fights to defending a territory. Some aspects may, however, be more critical to biparental species in which males contribute to the care of offspring and the function of the territory is for reproduction. Finally, we highlighted how these different behavioral mechanisms recruit neural circuits modulating social behavior (BNST), motivation (NAcc), and learning and memory (hippocampus). The studies we reviewed primarily examined these processes individually, and usually did not consider how behavioral effects might impact territory formation. It is likely that these nuclei work together in a coordinated fashion to shape territoriality. The ventral hippocampus has strong connections with both the NAcc (Eagle et al., 2015) and BNST (Cullinan et al., 1993), suggesting that social opportunities and winning experiences could have a coordinated impact on activity within these regions. Furthermore, T pulses following winning experiences (or successful mating opportunities) could be an additional mechanism through which salient social experiences can induce long lasting changes in behavior.

Historically, as the challenge hypothesis began to be tested in non-avian species, some of the initial results appeared to be quite different than expected (e.g. positive associations between parental behavior and aggression). With time, however, a better understanding of how aggression is used across contexts (mate acquisition vs offspring defense) has helped the hypothesis to evolve to explain behavior across a broader range of taxa. Further outlining of the mechanisms underlying challenge effects could lead to even more insights into how challenge effects have evolved across taxa. The challenge hypothesis was built as an idea to explain hormone-behavior relationships across different species of birds. However, three decades of rigorous evaluation of this hypothesis has proven that it can explain fundamental aspects of social behavior across a wide range of vertebrate taxa.

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