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Seasonal regulation of behaviour: what role do hormone receptors play?

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Many animals differentially express behaviours across the annual cycle as life stages are coordinated with seasonal environmental conditions. Understanding of the mechanistic basis of such seasonal changes in behaviour has traditionally focused on the role of changes in circulating hormone levels. However, it is increasingly apparent that other endocrine regulation mechanisms such as changes in local hormone synthesis and receptor abundance also play a role. Here I review what is known about seasonal changes in steroid hormone receptor abundance in relation to seasonal behaviour in vertebrates. I find that there is widespread, though not ubiquitous, seasonal variation in the expression of steroid hormone receptors in the brain, with such variation being best documented in association with courtship, mating and aggression. The most common pattern of seasonal variation is for there to be upregulation of sex steroid receptors with the expression of courtship and mating behaviours, when circulating hormone levels are also high. Less well-documented are cases in which seasonal increases in receptor expression could compensate for low circulating hormone levels or seasonal downregulation that could serve a protective function. I conclude by identifying important directions for future research.

1. Introduction

Even among casual observers, conspicuous changes in the behaviour of animals, such as birds singing in the spring, can signal a change of the season. Although not always dramatic, the differential expression of behaviours across the annual cycle is a widespread phenomenon among animals. These behavioural changes reflect the organization of the annual cycle into life-history stages, which allow animals to cope with variable environments and coordinate activities with suitable environmental conditions [1]. For example, breeding is typically timed such that the appearance of young coincides with relatively abundant food resources, and the transition from a non-breeding to breeding state is accompanied by behavioural shifts such as the onset of courtship and mating behaviours.

Traditionally, research aimed at understanding the mechanistic basis of changes in behaviour across the annual cycle (hereafter 'seasonal' changes) has focused predominantly on the role of changes in circulating hormone levels (figure 1*a*; [2,3–5]). This approach has led to important advances in our understanding of the seasonal regulation of behaviour. However, it has also revealed its limitations in cases where seasonal changes in behaviour occur independently of changes in circulating hormones [6–8]. At the same time, there has been growing attention to aspects of the endocrine system beyond modulation of circulating hormone levels that are important in regulating the expression of behaviour. Changes in local hormone synthesis or inactivation, including interconversion between active and inactive forms [9–12], hormone-binding proteins [13], receptor coactivators [14,15] and receptor abundance [16–18] have all been implicated in the regulation of behaviour. These modulation mechanisms may also be important in the seasonal regulation of behaviour. Thus, investigations of aspects of the endocrine system beyond circulating hormones represent important avenues for research aimed at advancing our understanding of the seasonal expression of behaviour.

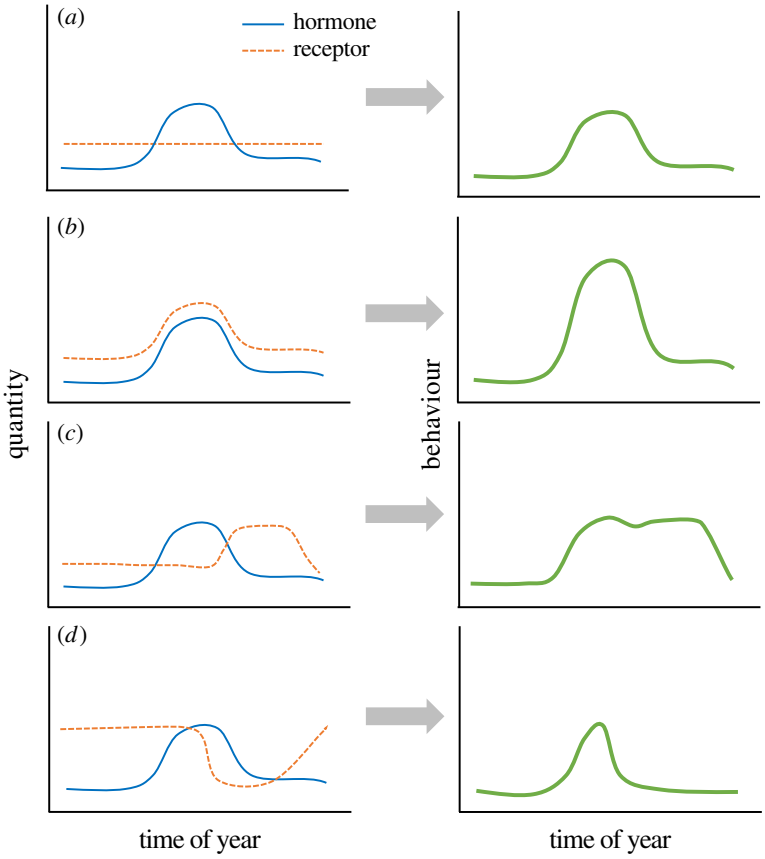

Figure 1. Potential relationships among seasonal changes in hormone receptor abundance, circulating hormones and behavioural responses. Four scenarios are shown in which the seasonal pattern of hormone secretion is the same, but the pattern of receptor abundance varies. For each scenario, the pattern of response (i.e. expression of a behaviour) generated by hormone-receptor binding is shown. (*a*) No seasonal changes in receptor abundance, variation in the behavioural response is driven entirely by changing hormone levels. (*b*) Enhancement: a seasonal increase in receptor abundance enhances the effect of the hormone. (*c*) Compensation: a seasonal increase in receptor abundance compensates for low hormone levels, sustaining expression of the behaviour when hormone level is low. (*d*) Protection: seasonal decline in receptor abundance reduces expression of behaviour despite high hormone levels. The scenarios shown are simplified for illustration; quantities of both hormones and receptors may further vary on timescales shorter than those shown here, and other regulatory elements such as hormone-binding proteins, hormone-metabolizing enzymes and receptor coactivators may also influence the behavioural response. (Online version in colour.)

In the context of understanding seasonal patterns of behaviour, the most widely studied endocrine mechanism beyond circulating hormones has arguably been receptor abundance. Binding of a hormone to its receptor is the mechanism by which a hormone elicits an effect on a target cell (e.g. by triggering changes in gene transcription or activating enzymes). Changes or differences in receptor abundance are an important element in the complex regulation of endocrine function—they facilitate differential sensitivity across tissues and over time, and they provide a means by which endocrine function can be modulated independently of hormone secretion. Moreover, receptor abundances are known to vary in response to environmental conditions during development [19,20] and in adulthood [21,22]. When we consider seasonal changes in receptor abundance within a given tissue, several broad functions have been hypothesized (figure 1). Increased receptor abundance could coincide with elevated circulating hormone levels, which could serve to enhance responsiveness (figure 1*b*; [23]). Alternatively, increased receptor abundance could serve to compensate for lower circulating hormone levels, allowing for the expression of a behaviour when circulating levels are low (figure 1*c*; [24,25]). Finally, seasonal reductions in receptor abundance could function to prevent or reduce the expression of behaviour at inopportune times, even if circulating hormone levels are elevated (figure 1*d*; [26]).

Here, I review what is known about seasonal changes in steroid hormone receptor abundance across phases of the annual cycle in vertebrates, with a focus on changes in the brain in relation to behaviour. Whereas I provide an overview of this literature below, a more comprehensive summary of relevant studies can be found in the electronic supplementary material, table S1. I have focused this review on receptors for steroid hormones—sex steroids and glucocorticoids—because these have been widely studied across species. I have included studies that quantify receptors directly by examining expression levels of the protein, as well as studies that measure mRNA expression as an indirect indicator of receptor abundance. However, it is important to recognize that mRNA level does not always predict the protein level because of variation in processes such as the rate of translation and protein turnover [27,28]. Here, I highlight themes that emerge from the literature, particularly in relation to potential functions, and identify important directions for future work.

2. Seasonal patterns of sex steroid receptor abundance

(a) Sexual behaviours

Efforts to understand the relationship between the seasonal expression of sexual behaviour and sex steroid receptors have often compared animals in breeding and non-breeding condition. A range of approaches have been used to do

this, from sampling free-living animals at different times of year to inducing breeding and non-breeding states in captive animals by manipulating photoperiod (day length). Such studies reveal many cases in which sex steroid receptors are elevated in brain regions associated with reproductive behaviour among animals in breeding condition compared to those in a non-breeding state. For instance, in goldfish (*Carassius auratus*), androgen receptor (AR) expression in the forebrain varies seasonally and is highest during the breeding season [29]. Both male and female ring doves (*Streptopelia risoria*) show elevated levels of AR and progestin receptor (PR) in brain regions associated with reproductive behaviours on long days, when birds are expressing courtship behaviour, compared to short days [30]. Similarly, neural AR expression is elevated in breeding condition male Syrian hamsters (*Mesocricetus auratus*) compared to those in non-breeding condition [31]. Yet, these seasonal elevations in association with breeding are not ubiquitous as a number of studies have found no differences in receptor expression. For example, in male and female green anoles (*Anolis carolinensis*), AR and oestrogen receptor (ER) α levels do not differ significantly between breeding and non-breeding seasons in brain regions that are important for sexual behaviour [23,32]. And although female Siberian hamsters (*Phodopus sungorus*) show seasonal variation neural ERα expression, this variation does not appear to be associated with reproductive behaviour [33]. Overall, the pattern that emerges across studies is that sex steroid receptors are often upregulated during the breeding season, suggesting that this could serve to enhance the responsiveness of tissues to circulating sex steroids when circulating levels are also high (figure 1*b*).

(b) Communication

Singing behaviour of songbirds, which can function in mate attraction and territorial defense, has served as a popular system for research examining the role of seasonal changes in steroid receptors. Testosterone is known to stimulate singing behaviour and the effects of testosterone appear to occur via activation of both ARs and ERs, following aromatization of testosterone to oestrogen [34]. The song control system of the songbird brain is an important area in which testosterone can act to exert these behavioural effects. The song control system consists of interconnected brain regions that regulate song learning and production, and many of these regions express ARs and/or ERs [34,35].

In cases where songbirds exhibit seasonal variation in singing behaviour, seasonal changes in the abundance of ARs in the HVC, a region of the song control system involved in both song learning and production, are generally observed—with abundance elevated when singing behaviour is expressed [36–39]. By contrast, black redstarts (*Phoenicurus ochruros*) show differences in singing behaviour between breeding and non-breeding periods, but do not show seasonal changes in AR levels in the HVC [40]. Compared to ARs, ERs exhibit less seasonal variation in abundance in the HVC [40,41] (but see [38,42]). Further, there is little seasonal variation in sex steroid receptor expression in other song control nuclei [37,40], though these have been less widely studied. Thus, the main pattern that emerges is that AR expression in the HVC is generally elevated in association with singing behaviour. But, variation among species suggests interspecific variation in the mechanisms responsible for regulating singing behaviour.

Although singing behaviour is largely limited to the breeding season in some species, in other species, singing behaviour is also expressed during non-breeding periods. In the latter case, birds may be singing even when circulating testosterone levels are low. This observation has led researchers to hypothesize that seasonal increases in sex steroid receptors facilitate the expression of singing behaviours during the non-breeding season (figure 1*c*; [24,25,36,41]). Studies of the song control system in three species of songbirds do not support this hypothesis—AR levels, and ER levels when examined, in the HVC in the autumn are similar to or lower than levels in the spring breeding period [36,37,40,41]. On the other hand, data from silver-beaked tanagers (*Ramphocelus carbo*) are consistent with a role for an increase in the number of AR target cells in the HVC in supporting singing behaviour early in the breeding season when circulating testosterone levels are still low [39]. Similarly, in male canaries (*Serinus canaria*) ER expression in the HVC is increased in the autumn non-breeding season compared to the breeding season, though AR and aromatase expression do not differ [38,42]. Thus, the sensitivity of this region to oestrogens appears to be elevated in the autumn, and the capacity to convert androgens to oestrogens is maintained.

Beyond birds, seasonal changes in sex steroid receptors in relation to communication and signalling have been examined primarily in fish. Electric fish use electric organ discharges in social communication, and this behaviour shows seasonal variation [43]. In the electric fish *Brachyhypopomus gauderio*, breeding males have greater AR expression in the area of the brain that regulates the rate of electric organ discharge compared to non-breeding males [44]. Thus, as in a number of the songbird studies, we see the upregulation of AR in a brain region closely linked to social signalling in parallel with the seasonal expression of the signalling behaviour. Work in an African cichlid (*Astatotilapia burtoni*) has documented changes in ARs and ERs in the inner ear and brain of females across the breeding season [45]. Though the exact functional significance of these changes is not yet clear, steroid hormones have been found to alter auditory sensitivity to vocal signals in other fishes [46]. Thus, one can hypothesize that these changes are related to seasonal changes in auditory function associated with receiving courtship signals and mate choice [45]. These results are intriguing and highlight an area of research that has received relatively little attention: the role of endocrine mechanisms in modulating seasonal changes in receiver sensitivity to signals such as those involved in courtship [47–49]. Further, given evidence for a role of androgens in seasonal communication behaviour in other vertebrate taxa (e.g. amphibians [48], mammals [50]), examining receptor expression in this context in a wider range of taxa is warranted.

(c) Aggression

Seasonal changes in sex steroid receptor expression have also been studied in efforts to understand seasonal patterns of aggression, particularly territorial aggression. Although vocalizations can function in territorial aggression as described above, I do not revisit those findings here. Most studies related to aggression have focused on species in which androgens and/or oestrogens are involved in regulating aggressive behaviours and yet aggressive behaviours are expressed at times of the year when circulating levels of these hormones are low. Thus, studies have mostly focused on whether there are compensatory changes in receptor expression (figure 1*c*) to facilitate the expression of aggressive behaviours.

Studies in birds have focused primarily on cases where territorial behaviour is expressed both during the breeding season and outside of the breeding season. Both androgens and estrogens play important roles in territorial aggression during the breeding season in birds, when circulating levels of these hormones are elevated [51]. Yet, in two species of birds that express territorial aggression in the non-breeding season when levels of circulating sex steroids are low, abundances of ERs and ARs are not elevated in brain regions involved in regulating aggression as would be expected if compensation is occurring. Instead, ER and AR abundances are similar to or lower than levels in the breeding season [41,52]. On the other hand, in spotted antbirds (*Hylophylax naevioides*), levels of ERs and ARs in brain regions involved in regulating aggression are elevated in males during the non-breeding season compared to the breeding season [25]. Although circulating testosterone levels remain relatively low throughout the year in this species, levels are lowest during the non-breeding season [53]. Therefore, the pattern in spotted antbirds is consistent with a compensatory mechanism by which increasing sensitivity to sex steroids could facilitate the expression of territorial aggression in the non-breeding season [25]. Overall, these studies suggest variation across bird species in the mechanisms regulating territorial aggression outside of the breeding season. This is consistent with evidence that territorial behaviours may be regulated independently of androgens and estrogens in some species and times of year [52,54].

Rodents have also served as models to investigate the relationship between sex steroid receptor expression and seasonal patterns of aggression. In these species, aggression is typically elevated on short, winter days when animals are not breeding and thus have low levels of gonadal sex steroids, and aggression is lower on summer days of the breeding season when circulating levels of gonadal steroids are high. In both male and female Siberian hamsters, which follow this pattern, ERα levels are elevated in brain regions involved in regulating aggression in animals on short days compared to long days [33,55]. Similar patterns have also been found in two species of *Peromyscus* mice. Specifically, Trainor *et al*. [56] found that ERα levels are elevated in the bed nucleus of the stria terminalis (BNST) and ERβ levels are reduced in BNST and medial amygdala in the winter compared to summer. These findings fit with hypothesized roles for ERα in mediating the stimulatory effects of estrogens on aggressive behaviour and ERβ in mediating inhibitory effects [57]. Overall, results from rodents suggest that seasonal changes ERs expression serve a compensatory function (figure 1*c*) to facilitate seasonal patterns of aggression in these species. However, experimental manipulations testing the relationship between ERs and aggression in *Peromyscus polionotus* using agonists specific for ERα and ERβ indicate that behavioural differences were not due to differences in nuclear ER expression [57]. Thus, the work of Trainor *et al*. [57] highlights the need for more such manipulative experiments to directly test causal relationships suggested by correlative seasonal patterns.

(d) Parental behaviours

Patterns of sex steroid receptor expression associated with parental behaviour have been investigated primarily in birds, and in ring doves in particular. Broadly, both male and female ring doves show changes in receptors associated with shifts from non-breeding or courting to incubation of eggs and brooding of young, with patterns being quite consistent between males and females. In both males and female ring doves, AR expression is high during courtship and lower during incubation and brooding across numerous brain regions [30,58]. Patterns of PR expression are more variable across brain regions and between the sexes. In the preoptic area, where progesterone is thought to act to mediate the expression of parental behaviour, PR expression is elevated in breeding doves compared to non-breeding doves [30,59]. However, the seasonal variation in PR expression in this region does not appear to tightly and consistently parallel the expression of parental behaviour across studies [30,59]. Finally, a study of female tree swallows (*Tachycineta bicolor*) using RNA-seq found that expression of a non-classical progestin receptor (PAQR9) was elevated during incubation compared to earlier in the breeding season when territories were being established in one brain region involved in the regulation of aggression and parental care [60]. However, no other steroid hormone receptors were differentially expressed seasonally in this study. Thus, limited studies of birds suggest that ARs may be downregulated and PRs may be upregulated in some cases to facilitate the expression of parental behaviour. However, more research is needed, particularly across a wider array of taxonomic groups.

3. Seasonal patterns of abundance of receptors for glucocorticoids

There are two classes of receptors for glucocorticoids: mineralocorticoid (type I) receptors (MRs) and glucocorticoid (type II) receptors (GRs). Intracellular MRs function primarily as high-affinity but low-capacity genomic receptors for glucocorticoids, whereas intracellular GRs function as low-affinity, high-capacity genomic receptors [61–63]. Additionally, there are less well-described membrane-bound receptors for glucocorticoids, which can mediate the rapid non-genomic effects of glucocorticoids [61,64]. In some cases, these membrane-bound receptors appear to be MRs and GRs [64], but in other cases, they have distinct binding specificities [65].

Considerable research has examined seasonal changes in GRs and MRs, primarily in the context of understanding seasonal changes in responses to stressors. Seasonal variation in glucocorticoid stress response is common in birds, reptiles, amphibians and mammals, though the specific pattern of variation can differ within and between these groups [3]. Actions of glucocorticoids in the brain are important in negative feedback to the hypothalamic–pituitary–adrenal/interrenal (HPA/I) axis [63,66,67] and in the regulation of behaviour [68–71], though few studies have attempted to link changes in receptor expression directly to seasonal changes in behaviour.

Seasonal changes in both GRs and MRs have been found at the level of the whole brain [72,73], as well as within the hippocampus and hypothalamus [74–76]—regions with potential roles in the regulation of behaviour and putative sites for negative feedback [63,66,67]. Studies of mammals (i.e. rodents) have found seasonal variation in MR expression, but not GR, with MR expression elevated in association with short days, torpor and hibernation [74,75,77]. In at least some species, MR levels are high when circulating glucocorticoids are reduced, consistent with a compensatory function

(figure 1*c*; [74]). Generally, studies of birds have found very little seasonal variation in the expression of GR and MR in the hippocampus or hypothalamus [60,73,76,78,79]. However, Krause *et al*. [76] found hippocampal MR levels dropped as male Gambel's white-crowned sparrows progressed from pre-parental to parental phases of the breeding season, paralleling observed reductions in stress-induced corticosterone as males become parental. Functionally, this could reduce responsiveness to corticosterone during the parental phase compared to breeding (figure 1*d*).

4. Conclusion and future directions

Across vertebrates there is widespread, though not ubiquitous, seasonal variation in the expression of steroid hormone receptors in the brain. These patterns have been best documented in association with seasonal expression of courtship, mating and aggression, with other stages and behaviours such as parental, migratory and hibernation ripe for future study. When we consider broad patterns of covariation between receptor expression, circulating hormone levels, and the expression of behaviour, we see that sex steroid receptor expression is often upregulated with the expression of courtship and mating behaviours (e.g. male singing in birds), when circulating hormone levels are also high. This pattern is consistent with a seasonally enhancing effect of receptor expression (figure 1*b*). On the other hand, seasonal changes in receptor expression that would facilitate compensation for low circulating hormone levels (figure 1*c*) do not appear to be common. However, the pattern does occur in some cases, such as in association with aggression in spotted antbirds [25] and Siberian hamsters [33,55]. The observed variation across species in these relationships is consistent with recent evidence that the endocrine system, and particularly tissue sensitivity to hormones as mediated by receptor abundance, is evolutionarily labile [80,81]. Empirical studies that evaluate a potential protective effect of seasonal downregulation of receptors have been far fewer, though patterns consistent with such a role have emerged in association with the parental stage [76]. This review has also illustrated that there are numerous cases in which seasonal changes in behaviour occur in the absence of concomitant changes in steroid hormone receptors. This observation highlights the need for future work to examine other mechanisms that may drive seasonal differences in the expression in behaviour, several of which are highlighted below.

Although I have focused on steroid hormone receptors, investigations of other receptor types will also be critical to understanding seasonal changes in behaviour. Non-steroid hormones play a prominent role in regulating many behaviours and may interact with steroid hormones to influence the expression of behaviour. In the case of parental behaviour, differential expression of prolactin receptors may play a role [82]. Similarly, changes in receptors for oxytocin and arginine vasopressin (and their homologues) may be important in modulating seasonal patterns of social behaviour [83–85], and seasonal changes in melatonin receptor expression have been associated with reproductive behaviour in birds [86] and hibernation in mammals [87].

The role of seasonal changes in other regulatory points on endocrine signalling pathways also warrants further investigation. For example, seasonal changes in the expression of aromatase in the brain and circulating corticosteroid-binding globulin (CBG) levels are prime candidates. Changes in the expression of aromatase, which catalyses the conversion of testosterone to oestradiol, are a mechanism by which local availability of estrogens can be modulated. Aromatase activity is known to be critical for the expression of behaviours such as male aggression and sexual behaviours [88–90], and seasonal changes in aromatase expression in the brain have been documented across a wide range of vertebrates [91–94]. CBG is a hormone-binding protein that binds glucocorticoids with high affinity, and other steroid hormones with lower affinity [13]. CBG likely plays a role in transporting glucocorticoids and mediating the access glucocorticoids have to tissues, though its exact function remains a topic of debate [13,95,96]. Nonetheless, CBG binding capacity has been found to vary seasonally in both birds and mammals [97–100]. More broadly, research that simultaneously investigates multiple aspects of endocrine regulation (e.g. circulating hormone levels and hormone-binding proteins, as well as hormone synthesis/metabolism and receptor abundance at target tissues) will allow for a more holistic understanding of seasonal regulation (e.g. [101]). Such an approach may be especially useful in advancing our understanding of the regulation of some seasonal behaviours, such as migration, for which a focus on circulating hormones levels has provided only limited insight thus far [102].

This review has focused on seasonal changes in neural steroid receptors as a mechanism mediating seasonal changes in behaviour. However, there is a growing appreciation of the importance of hormone action in peripheral tissues in the regulation of behaviour [103]. Variation across species, sexes and individuals in levels of AR expression in peripheral tissues have been associated with differential expression of a variety of behaviours. For example, AR expression in muscles covaries with the expression of courtship display in birds [104], social and sexual behaviour in fish [105], and display and locomotor behaviours in lizards [106]. In birds, experimental manipulations have confirmed a functional link between peripheral AR activation and courtship and vocal behaviours [107,108]. Despite, this growing understanding of the action of steroid hormones in the periphery in the expression of behaviour, studies examining their role in seasonal patterns of behaviour are currently few. Maruska & Fernald [45] have found seasonal differences in steroid receptors of the peripheral auditory system in a cichlid fish—a species that uses auditory cues in social interactions. Pradhan *et al*. [109,110] documented differences in the expression of ARs and MRs in skeletal muscles across a seasonal migratory transition in birds. Further, in muskrats (*Ondatra zibethicus*), Lu *et al*. [111] have found seasonal variation in AR expression in the scent gland, which is used in mate attraction. However, in all three examples, receptor variation has not yet been directly linked to behavioural variation.

As this review has highlighted, there is now ample evidence that the expression of hormone receptors can vary seasonally. However, more work is needed to determine the functional significance of this variation for the expression of behaviour. In some cases, greater anatomical resolution is needed to determine the specific locations where receptor expression is changing. In other cases, detailed behavioural data are needed to pair with information about receptor expression. For example, much of the research on seasonal patterns of GR and MR expression has focused on the regulation of the HPA/I axis, with much less attention paid to the potential

significance for behaviour. More broadly, the vast majority of research to date has been correlational in nature—examining patterns of covariation between the expression of receptors and behaviour. A critical next step will be to perform experimental manipulations to determine whether these correlations reflect causal relationships. Pharmacological approaches using receptor agonists or antagonists can be used to test whether blocking or activating the receptor of interest produces the expected change in behaviour (e.g. [57]). Another set of approaches, increasingly available in non-model systems, involve manipulating expression a receptor by targeting its gene. These include more established approaches to reduce receptor expression, such as RNA interference [112] or antisense oligonucleotides [113], and gene transfer to enhance expression of a receptor [114]. Emerging CRISPR–Cas9 gene-editing techniques can also be used to manipulate gene expression (e.g. CRISPR-based activation (CRISPRa) and interference (CRISPRi)) and show promise for use in the adult brain [115,116]. Techniques that allow for manipulation of receptor expression or activation within ranges observed seasonally (e.g. knockdown rather than knockout) will be best suited for testing hypothesized relationships—in this regard, the genetic approaches highlighted above, notably CRISPRa/i, are particularly promising.

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