

Operant light self-administration in mice and its relevance to digital technology-based disorders

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VIEWPOINT



ABSTRACT

Behavioral addictions share symptomatological features with substance addiction. From the associative learning perspective, these characteristics include excessive and unregulated self-administration of sensory and other reinforcers, potentially reflecting the transition from goal-directed actions (*action* → *outcome* associations) to habitual responses (*stimulus* → *response* associations). In laboratory mice, light stimulation at an optimal intensity possesses some incentive properties and a brief light pulse represents an effective reinforcer for persistent operant responding. The operant light self-administration paradigm with clearly defined sensory reinforcers and reinforcement schedules may be utilized to elucidate the general mechanisms of excessive habitual responding to seek non-drug and non-feeding cues in mice. This cross-species approach can shed light on some maladaptive habits that have emerged recently in our modern society, including digital technology-based disorders.

KEYWORDS

behavioral addiction, rodents, instrumental conditioning, light reinforcer, habit, smartphone use, mobile phone use

INTRODUCTION

Habit formation has been studied in humans and laboratory animals since the time of Hull (1934a, 1934b). We form habits toward many primary reinforcers and conditioned incentives; some habits are highly adaptive and essential for survival, whereas others may not serve any obvious function and even interfere with our daily lives.

Maladaptive habit formation has been linked to symptoms of behavioral addiction including digital technology-based disorders (e.g., Zhou et al., 2024). An example is Internet-use disorder (Wegmann, Billieux, & Brand, 2022), which refers to excessive and ultimately compulsive use of the Internet (Brand, 2022; Brand et al., 2024; Fineberg et al., 2022) and encompasses conditions such as smartphone use and gaming disorder (Duke & Montag, 2017; Giordano et al., 2020; Holm, Prosek, Bennett, & Sims, 2021; Kaptsis, King, Delfabbro, & Gradisar, 2016; van Velthoven, Powell, & Powell, 2018). These conditions have received increasing attention from clinicians and mental health professionals in recent years due to a surge in prevalence especially among children and adolescents (Kim et al., 2022; Lopez-Fernandez, Honrubia-Serrano, Freixa-Blanxart, & Gibson, 2014; Marshall, Warburton, & Kangas, 2022; Meng et al., 2022; Montag & Becker, 2024; Montag, Schulz, et al., 2024; Montag, Demetrovics, et al., 2024; Stevens, Dorstyn, Delfabbro, & King, 2021). The etiology and features of these conditions are complex and multifaceted, and they are highly heterogeneous across

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individuals who often exhibit psychiatric comorbidities (Bilieux, 2012; González-Bueso et al., 2018; Ioannidis et al., 2018; Király, Koncz, Griffiths, & Demetrovics, 2023). However, in certain domains such as gaming disorders, emerging evidence suggests that they share some core symptoms with substance addiction. Most notably, these include preoccupation with use, loss of control, and continued use despite negative consequences (Giordano et al., 2020; Holm et al., 2021; Kaptis et al., 2016). Some recent studies have suggested that Internet addiction may involve excessive and habitual self-administration of sensory reinforcers of different modalities (Gera, Barak, & Schonberg, 2023; Tian, Bi, & Chen, 2023), thus partly resembling other types of behavioral addiction (Robbins & Clark, 2015).

In this article, we will use some behavioral addictions in particular digital technology-based disorders, such as Internet-use disorders, as an example to suggest how certain maladaptive habits in modern-day environments can be modeled in laboratory rodents. An advantage of a cross-species approach is that it allows the use of a wider range of

methods (Fig. 1 and Table 1) to study the general mechanisms of maladaptive habit formation involving the use of digital devices; the shortcomings of this will be discussed below. Cross-species approaches may also be utilized to study the mechanisms of other maladaptive habits, such as gambling disorder (de Visser et al., 2011; Kim, Cho, Kwak, & Kim, 2017; Pais-Vieira, Lima, & Galhardo, 2007; Rivalan, Coutureau, Fitoussi, & Deltu-Hagedorn, 2011; Zeeb, Robbins, & Winstanley, 2009), provided that relevant reinforcers and reinforcement schedules can be identified and operationalized in experimental studies; this remains one of the major challenges in the field of behavioral addiction (James & Tunney, 2017; Tunney & James, 2017). In line with previous literature, here we will use the term Internet-use disorder to refer to the clinical condition (Wegmann et al., 2022) and the term Internet addiction to refer to the underlying processes (Zhou et al., 2024), for example, maladaptive habits that can potentially be examined in animal models.

Progress in understanding the general mechanisms of addiction has been driven by sophisticated animal models

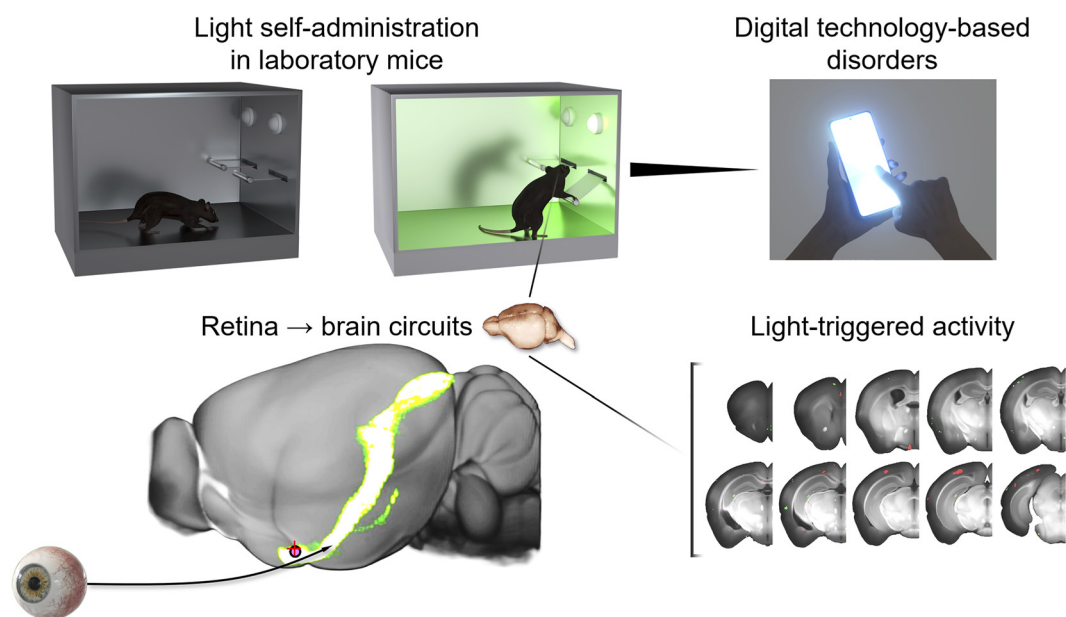


Fig. 1. The mouse light self-administration paradigm as a simplified model for digital technology-based disorders

Top panel: In mouse free-operant light seeking experiments, fixed-ratio (FR) reinforcement schedules (x responses:1 reinforcer, where x is the response requirement) are often used to establish steady responding to light reinforcers (Helfand et al., 2017; Olsen et al., 2010; Olsen & Winder, 2009, 2010; Parkitna et al., 2013; Sikora et al., 2019). The reinforcer can be a white light or monochromatic light, although the reinforcing properties of different features of light (e.g., light duration, light intensity, and spectral composition) have not been systematically examined in previous studies. One lever is assigned as the active, reinforced operandum (Lever+), and the other lever is assigned as the inactive, nonreinforced operandum (Lever-). The assignment of Lever+ and Lever- is counterbalanced across mice but remains unchanged for each mouse during the experiment. Operant light seeking can be assessed using different measures, such as the rate of responding on Lever+, the rate of reinforcer delivery, and the extent of operandum discrimination between Lever+ versus Lever-. *Bottom panels:* By utilizing a cross-species approach, we can use a wider range of methods to investigate the general mechanisms underlying digital technology-based disorders that are partly triggered by light (see also Table 1). In the *bottom left* panel, the mouse brain image shows retina → brain projections to multiple retinorecipients in the hypothalamus, thalamus, and midbrain via the optic tract. Projection data are obtained from tracing experiment 306957248 in the Allen Mouse Brain Connectivity Atlas database. Image credit: Allen Institute for Brain Science [<https://connectivity.brain-map.org/projection/experiment/306957248>]. The roles of these circuits in driving light self-administration can be examined by using methods such as chemogenetics. In the *bottom right* panel, mouse brain areas that are activated by light (as measured by an increase in cFos proteins) are colored in red (e.g., the primary visual cortical areas and hypothalamic retinorecipients), whereas areas with cFos reduction are colored in green (e.g., the entorhinal cortical areas)

Table 1. The mouse light self-administration paradigm as a simplified model for digital technology-based disorders: future research questions

Example Research Questions	Methods
(a) How does the reinforcing effectiveness of light vary as a function of light duration, light intensity, spectral composition, and mode of delivery (operant <i>vs.</i> non-operant procedure)?	E
(b) What are the photoreceptors (rods/cones <i>vs.</i> photosensitive retinal ganglion cells) and <i>retina</i> → <i>brain</i> circuits that encode the incentive values and hedonic properties of light of different wavelengths?	C,G
(c) Is the operant light seeking response modulated by behavioral context? What will happen if a concurrent choice (lever pressing for light <i>vs.</i> retreating into a dark nestbox) is available in the test chamber?	E
(d) In addition to the key neurotransmitters and receptors reviewed in the main text, what are the roles of other neurotransmitters (e.g., GABA) and neuromodulators (e.g., serotonin) in operant light seeking?	G,P
(e) How is operant light seeking influenced by biological age, sexual dimorphism, and genetic polymorphism? Does any of these effects occur <i>via</i> dopamine, glutamate, endogenous opioid, or other receptor signaling?	G,P
(f) What are the relative contributions of biological (e.g., biological age, sexual dimorphism, or genetic polymorphism) <i>vs.</i> environmental factors (e.g., home cage enrichment, test chamber enrichment) to operant light seeking?	E,G,P
(g) Is there any long-term consequence of light-triggered maladaptive habitual behavior for brain health, including its effects on cognition, sleep/wake pattern, and circadian rhythm?	E,H
(h) How does light-triggered maladaptive behavior interfere with brain development and corresponding social and cognitive development?	C,E,H
(i) Do learning mechanisms and underlying brain circuits differ between light-induced behavioral maladaptation <i>vs.</i> substance-induced maladaptation?	C,G,P
(j) Can targeting specific neurotransmitter systems prevent or facilitate the development of light-induced habit?	C,G,P

Note—C: Circuit tracing and chemogenetic manipulation; E: Environmental manipulation; G: Genetically altered mouse models; H: Home cage activity monitoring; P: Pharmacological manipulation.

and translational neuroimaging studies in humans, leading to a reconceptualization of addiction as a brain-based disorder (Everitt & Robbins, 2005, 2016; Koob & Volkow, 2016). Despite the growing number of studies examining Internet addiction from clinical (Pontes, Kuss, & Griffiths, 2015) and neuroimaging perspectives (Montag & Becker, 2023; Weinstein & Lejoyeux, 2020), currently there is no preclinical animal model to study Internet addiction. Although some researchers have recently questioned the value of animal models for addiction in general (Field & Kersbergen, 2020; Heather, 2018), mechanistic animal models often complement and stimulate progress in human addiction research (Deroche-Gamonet, 2020; Perry & Lawrence, 2020). Combining both approaches can provide a more holistic view of general addiction mechanisms, shedding light on the ongoing debate regarding the common and distinct brain pathways in substance *versus* non-substance addiction (Marraudino, Bonaldo, Vitiello, Bergui, & Panzica, 2022; Montag & Becker, 2023; Robbins & Clark, 2015).

Over the last two decades, addiction research has been guided by the seminal framework proposed by Robbins and colleagues, who postulate that the transition from initial (volitional) drug use to habitual and ultimately drug seeking is underpinned by the interaction between Pavlovian (classical) *versus* instrumental (operant) conditioning processes (for review see Dickinson, 1985; Everitt & Robbins, 2005; Ostlund & Balleine, 2008; Robbins & Clark, 2015; Everitt & Robbins, 2016). Based on their framework, excessive self-administration of a drug reinforcer is thought to reflect the transition from goal-directed actions (driven by *action* → *outcome* associations and are thus sensitive to outcome devaluation) to habitual responses (driven by *stimulus* → *response* associations), although this view has been challenged by recent human studies (Hogarth, 2020). Another influential framework is the iRISA (*Impaired Response Inhibition and Salience Attribution*) model developed by Goldstein and colleagues, who propose that different phases of the drug addiction cycle (drug use, withdrawal, and relapse) are driven by abnormal activity in multiple cortical and subcortical circuits regulating behavioral inhibition and aberrant salience; these are reviewed in detail elsewhere (Goldstein & Volkow, 2002, 2011; Zilverstand, Huang, Alia-Klein, & Goldstein, 2018). These frameworks from drug addiction have been expanded in recent years to incorporate Internet addiction, notably the I-PACE (*Interaction of Person-Affect-Cognition-Execution*) model formulated by Brand and colleagues (Brand, Young, Laier, Wölfling, & Potenza, 2016; Brand et al., 2019).

Animal studies of addiction utilize classical and operant conditioning paradigms, in which drugs and drug-associated cues (such as context) are used as primary reinforcers and conditioned reinforcers, respectively (Hogarth, 2020). While these paradigms allow to model human substance use patterns and the development of substance addiction behavior in experimental animals, corresponding models for Internet addiction are more challenging to develop. The major obstacle represents the possibility of multiple plausible reinforcers (primary or conditioned) and schedules of

reinforcement (fixed-ratio, variable-ratio, or random-ratio schedules) that could give rise to various subtypes of maladaptive behavior (cf. James & Tunney, 2017; Tunney & James, 2017). Moreover, effective reinforcers in Internet addiction such as cognitive, affective, sexual, and social cues are often difficult to quantify and operationalize in experimental studies of instrumental conditioning (although see Ramsey, Holloman, Lee, & Venniro, 2023; Venniro & Shaham, 2020 for the operant social self-administration task in rats and mice). Apart from these reinforcers, sensory reinforcers such as light and sound (Olsen & Winder, 2010) and novel everyday objects possess some reinforcing properties in rodents (Bevins & Bardo, 1999; Bevins et al., 2002); these are relevant to sensory self-administration in humans and easier to deliver to experimental animals. Thus, it is possible to modify the behavior of a laboratory animal and induce persistent responding using non-drug and non-feeding cues under traditional schedules of reinforcement (Olsen & Winder, 2009, 2010).

In laboratory mice, brief light pulses can serve as positive sensory reinforcers. Like drug administration, the dose of light administration (including its duration and light intensity) and instrumental contingency (*i.e.* the causal relationship between a preceding action and light delivery) can be precisely controlled by the experimenter, thus allowing us to adopt established rodent operant conditioning paradigms from substance to non-substance addiction research. Notably, the *operant sensation seeking* paradigm—in which a laboratory rodent persistently performs a self-paced instrumental response (e.g., lever pressing, nose poking, or touchscreen responding) to obtain a brief sensory reinforcer (e.g., a few seconds of light)—may provide an initial step to understand the general mechanisms of Internet addiction, which involves exposure to artificial light *via* LED screens. Furthermore, traditional operant conditioning paradigms can be combined with contemporary neuroscience techniques such as optogenetics and chemogenetics, permitting cell-type specific manipulations to identify brain circuits driving (excessive) sensory self-administration in healthy animals and animal models for addictive disorders (cf. Giannone et al., 2022); some candidate circuits from the retina to subcortical regions are highlighted in the next section.

NON-VISUAL EFFECTS OF LIGHT: ITS INCENTIVE VALUE AND HEDONIC PROPERTY

Among sensory reinforcers of different modalities, light cues may exacerbate habitual operant responding and strengthen maladaptive behavior (cf. behavioral addiction to fruit machines with multicolored light stimulation; Griffiths, 1993). The role of light is supported by emerging observations that applying grayscale filters on the smartphone is sufficient to reduce total smartphone screen time by at least 20–50 min per day in young adults (Dekker & Baumgartner, 2023; Holte & Ferraro, 2020; Holte, Giesen, & Ferraro, 2023;

Wickord & Quaiser-Pohl, 2023; Zimmermann & Sobolev, 2023). These preliminary findings indicate that artificial light (e.g., perceived color) may partly contribute to excessive engagement with digital operanda. However, it is unclear whether artificial light serves as: (a) a primary reinforcer that is intrinsically rewarding (Navarick, 1985); (b) a Pavlovian excitator, which is associated with other primary reinforcers and thus serves as a conditioned incentive for responding (Dayan & Balleine, 2002); or (c) a stimulus that causes a general increase in responsiveness due to a change in arousal, alertness, or affective state (Souman, Tinga, Te Pas, van Ee, & Vlaskamp, 2018; Weil, Zhang, Hornung, Blizard, & Pfaff, 2010). Specifically, if light can indeed serve as a primary reinforcer, learning about a light reinforcer should conform to the same formal learning rule (*i.e.* the reward prediction error term in the Rescorla–Wagner model) as typical reinforcers such as food or water; this remains to be examined in future studies. In any case, these non-visual effects of light are not mutually exclusive and may all contribute to excessive responding.

Although further investigations are required to delineate the role of light in determining smartphone use, animal studies can elucidate the general mechanisms that drive behavioral responses to light (Tam, Bannerman, & Peirson, 2020), thus providing some insights into the cause of light-induced excessive responding in mammalian species. In mice, the retina conveys light signals to subcortical circuits involved in reward and affective processes, thereby regulating hedonic behavior. These recently discovered functional circuits include: (a) the *retina* → *thalamic perihabenular nucleus* (PHb) → *nucleus accumbens* (NAc) circuit (An et al., 2020; Fernandez et al., 2018; Weil et al., 2022); (b) the *retina* → *lateral geniculate nucleus* (LGN) → *lateral habenula* (LHb) circuit (Huang et al., 2019); and (c) the *retina* → *central amygdala* (CeA) circuit (Wang et al., 2023). Some of these subcortical targets, such as NAc, LHb, and CeA, are known to regulate drug seeking behavior (Everitt & Robbins, 2005, 2016; Mathis & Kenny, 2019). In addition, exposure to artificial lighting, such as 305–310 nm ultraviolet, 472 nm blue, or 525 nm green light, can induce a hedonic behavioral state, producing “addiction-like” responses and relieving nociceptive pain in mice. These effects of lighting require endogenous opioid receptor signaling, in particular μ and δ (but not κ) opioid receptors (Fell, Robinson, Mao, Woolf, & Fisher, 2014; Ibrahim et al., 2017; Martin et al., 2021; Tang et al., 2022). Furthermore, in instrumental (operant) conditioning experiments where light is presented as a discrete cue, it can effectively reinforce behavioral choice in mice (see **Comparing light versus drug reinforcers**). Crucially, operant light seeking requires receptors (see **Receptors regulating light self-administration**) that are also involved in operant drug seeking (Koob & Volkow, 2016).

Given these findings, we suggest harnessing the reinforcing properties of light and utilizing the light self-administration paradigm (Fig. 1, top panel) to elucidate the general mechanisms of excessive habitual responding to seek non-drug and non-feeding cues, which partly resembles some

maladaptive habits in Internet addiction. This provides a simplified, albeit imperfect, model “that is free from the influence of culture, language, social reinforcement, and other experiential biases” specific to humans (Zentall, 2023, p. 1).

LIGHT SELF-ADMINISTRATION IN LABORATORY RODENTS

Instrumental (operant) conditioning

In non-aversive free-operant behavioral tasks (Mackintosh, 1974), animals perform a self-paced instrumental response, such as lever pressing, nose poking, or touchscreen responding, to trigger delivery of a certain reward. Various types of reward can be used to support operant responding. For example, in typical appetitive tasks where animals are either food or water restricted and thus motivated to obtain these resources, the reward is often delivery of a small food pellet or a drop of water or sweet-tasting solution; whereas in drug self-administration studies, the reward is direct intravenous infusion of a small amount of psychostimulant, alcohol, or any substance with addictive properties (Belin-Rauscent, Fouyssac, Bonci, & Belin, 2016). Intracranial electrical or optogenetic stimulation of the medial forebrain bundle, mesolimbic, or nigrostriatal circuit is also intrinsically reinforcing and can establish operant responding (Wise, 1996, 2005; Wise & McDevitt, 2018). However, a consumable reward, an addictive drug infusion, or brain stimulation is *not* necessarily required for acquisition and maintenance of operant responding. In fact, just a brief sensory stimulation, such as a few seconds of light in an otherwise dark operant chamber, is sufficient to support operant conditioning in laboratory rodents (Fig. 1, top panel). An effective light reinforcer can either be a few seconds of constant illumination (Stewart, 1960) or a salient light flicker that varies in terms of its frequency, duration, and spatial position in the operant chamber (Olsen & Winder, 2009, 2010). Light self-administration is also reported in home cages, where mice are permitted to voluntarily increase the light level in their cages *via* a nose poke operandum (Ogasawara et al., 2024).

Reinforcer intensity and dose

One of the earliest demonstrations of operant light seeking was by Stewart (1960), who reported rapid acquisition of lever pressing responses to light in rats under fixed-ratio (FR) reinforcement schedules (*i.e.* x responses:1 reinforcer, where x is the response requirement). After operant conditioning, during two days of extinction where light was no longer delivered, lever responding dropped slightly but was maintained at a level higher than baseline responding before conditioning. Crucially, lever responding during the extinction phase was light-intensity dependent, with the highest responding found in rats that were trained with the brightest light (Stewart, 1960). Although rats in her original study were food restricted, other studies reported similar operant sensation seeking responses in non-food-restricted

animals. Indeed, a light-intensity-dependent increase in lever pressing for 10-s white light of 1, 10, and 100 lux is observed under FR1 (1 response:1 reinforcer) in mice housed under food/water *ad libitum* conditions (L.C.E. Steel, S.K.E. Tam, D.M. Bannerman, & S.N. Peirson, *unpublished data*), confirming Stewart's (1960) original result. Thus, the reinforcing effectiveness of a light cue that is contingent upon an operant response is “light-dose” dependent, just like the dose-dependent reinforcing effects of intravenous self-administration of cocaine (Roberts, Casal, Huitron-Resendiz, Thompson, & Tarantino, 2018) and corticosterone (Piazza et al., 1993). Nevertheless, in nocturnal rodents the relationship between the magnitude of operant response and light intensity of the light reinforcer is likely to be inverted-U shaped, with an initial light-intensity-dependent rise in the light seeking response followed by an opposing light-induced anxiogenic response under brighter light (Ishida et al., 2005; Milosavljevic, Cehajic-Kapetanovic, Procyk, & Lucas, 2016; Semo et al., 2010; Steel, Tam, Brown, Foster, & Peirson, 2024; Thompson, Lupi, Hankins, Peirson, & Foster, 2008; Wang et al., 2023; Warthen, Wiltgen, & Provencio, 2011).

Reinforcer variability and complexity

In mouse operant light seeking studies, the typical visual reinforcer is a brief presentation of a flickering light with varying frequency, duration, and spatial position (Helfand, Olsen, & Hillard, 2017; Olsen, Childs, Stanwood, & Winder, 2010; Olsen & Winder, 2009, 2010; Parkitna et al., 2013; Sikora, Skupio, Jastrzebska, Rodriguez Parkitna, & Przewlocki, 2019). For example, Olsen and Winder (2009) used a multimodal visual-auditory compound reinforcer, in which the auditory component of the compound was always the same (a sound generated by the activation of an infusion pump motor outside the operant chamber), but the light component varied in duration (2, 4, 6, or 8 s), flickering frequency (0.625, 1.25, 2.5, or 5 Hz), and spatial position (left or right). Although the effectiveness of visual *versus* auditory reinforcers was not examined in their study, operant responding was likely to be driven primarily by the constantly varying (*i.e.* more salient) light reinforcer, but much less so by the unchanging (*i.e.* less salient) auditory component (*cf.* McSweeney & Murphy, 2009). Other multimodal sensory cues, such as brief retraction and insertion of the lever, can potentiate the effectiveness of light reinforcers and enhance operant responding in mice (Dickson & Mittleman, 2020). Similarly, in rats a brief light-tone compound reinforcer can potentiate the reinforcing effectiveness of nicotine infusion (Caggiula et al., 2002) and optogenetic stimulation of dopamine neurons in the ventral tegmental area (VTA) (Wolff & Saunders, 2024). Thus, the overall effectiveness of a reinforcer depends on its complexity, and the reinforcing effectiveness of light combined with other reinforcers are *additive* in nature.

Comparing light versus drug reinforcers

In operant conditioning tasks, the effectiveness of a reinforcer can be assessed under a progressive-ratio (PR)

schedule, in which the response requirement for earning the next reinforcer increased progressively after each reinforcer delivery. The maximum number of operant responses resulting in reinforcer delivery within a session is the *breaking point*, a measure of the animal's motivation to obtain the reinforcer. For example, in [Olsen and Winder \(2009\)](#), after initial FR1 training mice received a PR test schedule, in which the response requirement for light increased from 1, 2, 4, 6, 9, 12, 15, 20, 25, 32, 40,... according to $5e^{(0.2 \times i)} - 5$ where i denotes delivery of the i^{th} reinforcer ([Richardson & Roberts, 1996](#)); the breaking point for light reinforcers was ~ 40 lever presses ([Olsen & Winder, 2009](#)). To put this into perspective, this is comparable to the breaking point for high-sugar and high-fat food pellets (~ 20 – 60 lever presses depending on feeding regime; [Sharma, Hryhorczuk, & Fulton, 2012](#)), but it is lower than the breaking point for 0.5 mg/kg cocaine self-administration in the same mouse strain (~ 100 lever presses; [Roberts et al., 2018](#)).

However, under certain conditions light reinforcers can be as effective as addictive drugs in guiding behavioral choice in mice. In [Moussawi et al. \(2020\)](#), different groups of mice were trained under FR1 with either 1-min delivery of light, a vapor consisting of glycerol, or vaporized synthetic opioid fentanyl (2.5 mg/mL) as a reinforcer for nose poking response. Discrimination performance on active (correct) versus inactive (incorrect) operanda was expressed as a ratio score, $(N_{\text{correct}} - N_{\text{incorrect}})/(N_{\text{correct}} + N_{\text{incorrect}})$. As expected, the glycerol group showed almost no discrimination performance with an average score of ~ 0.05 . By contrast, light and fentanyl groups showed equally robust discrimination performance with scores of ~ 0.4 under FR1. But when task demand was increased from FR1 (1 response:1 reinforcer) to FR10 (10 responses:1 reinforcer), the fentanyl group showed an improvement in discrimination performance with an average score of ~ 0.6 , whereas performance in the light group remained unchanged. This indicates that, under less demanding task conditions, light can be as effective as addictive substances in guiding operant choice. Although [Moussawi et al. \(2020\)](#) did not further investigate the differential effectiveness of light versus drug reinforcers in their study, this is likely to be task specific and partly dependent on task parameters such as light intensity (see **Reinforcer intensity and dose**), light duration, and the spectral composition of light ([Pilorz et al., 2016](#)). It may also depend on whether the light reinforcer is presented as an increase in background irradiance versus a spatially localized cue, resulting in different levels of salience ([Bonardi, 2001](#)) and different learning rates.

RECEPTORS REGULATING LIGHT SELF-ADMINISTRATION

By using pharmacological manipulations and genetically altered mouse strains, several studies have identified the key receptors involved in operant light seeking, some of which

also play a role in operant drug seeking ([Koob & Volkow, 2016](#)) but not necessarily operant responding to typical appetitive reinforcers.

Dopamine receptors

Operant light seeking performance is sensitive to dopamine D1/2 receptor antagonist *cis*-flupenthixol. Intriguingly, [Olsen and Winder \(2009\)](#) reported that a relatively low dose of *cis*-flupenthixol (0.03 mg/kg) increased operant light seeking responses by 50% relative to baseline performance. This could be due to the reduced reinforcing effectiveness of light after reduced dopamine signaling, so that animals needed to receive more light reinforcers to compensate for attenuated sensory stimulation. By contrast, higher doses of *cis*-flupenthixol (0.15 and 0.21 mg/kg) reduced responding in both trained and untrained mice, indicating a general reduction in motivation for operant responding with a further decrease in dopamine signaling. In particular, the dopamine D1 receptor (D1R) is necessary for operant light seeking, as [Olsen and Winder \(2009\)](#) found that *Drd1a*-knockout mice lacking the D1 receptor gene *Drd1a* were unable to acquire operant responding to light under FR1 and showed no discrimination between active (Lever+) versus inactive (Lever-) operanda. By contrast, when *Drd1a*-knockout mice were food restricted, they were able to acquire operant responding to vanilla milkshake under FR1, showing discrimination performance between Lever+ versus Lever- comparable to control animals ([Olsen & Winder, 2009](#)).

Glutamate receptors

Using identical operant procedures, [Olsen et al. \(2010\)](#) examined the role of metabotropic glutamate receptor mGluR5 in operant light seeking in mice lacking the *Grm5* gene. These *Grm5*-knockout mice showed some limited discrimination performance between Lever+ versus Lever-, but their asymptotic responding on Lever+ was well below that of control animals. Under PR, the breaking point achieved by *Grm5*-knockout mice was ~ 4 lever presses, which was lower than the breaking point of their control counterparts (≥ 20 lever presses). Like *Drd1a*-knockout mice in [Olsen and Winder \(2009\)](#), *Grm5*-knockout mice in [Olsen et al. \(2010\)](#) were able to acquire operant responding to vanilla milkshake under FR1 when animals were food restricted.

Further evidence suggests that the interaction between D1R and mGluR5 is crucial for operant light seeking. This is demonstrated by [Parkitna et al. \(2013\)](#), who used a mouse model (*Grm5*^{D1}) in which expression of *Grm5* mRNA and mGluR5 protein was reduced by 50% in D1R-expressing medium spiny neurons (MSNs) in the dorsal striatum and nucleus accumbens; these MSNs co-expressing D1R and mGluR5 project to the substantia nigra (SN) and VTA ([Novak et al., 2010](#)). Like *Drd1a* and *Grm5*-knockout mice ([Olsen et al., 2010](#); [Olsen & Winder, 2009](#)), acquisition of operant light seeking was impaired in *Grm5*^{D1} mice, but operant food seeking was unaffected ([Parkitna et al., 2013](#)). Thus, glutamate-dopamine signaling by mGluR5 localized

in SN/VTA-projecting D1R striatal neurons is crucial for operant light seeking.

Opioid receptors

In addition to dopamine and glutamate signaling, operant light seeking requires endogenous opioid signaling. Using identical operant procedures as in previous studies, [Sikora et al. \(2019\)](#) examined the effects of nonselective and selective μ , δ , and κ opioid receptor antagonists on operant light seeking performance in mice. Nonselective opioid receptor antagonist naltrexone administered before test sessions reduced nose-poking responses to light by 50% relative to the saline condition at the intermediate dose (2 mg/kg), but lower (0.5 mg/kg) and higher doses of naltrexone (4 and 10 mg/kg) had no effect. Selective μ opioid receptor antagonist cyprodime caused a linear dose-dependent impairment; the highest dose of cyprodime (10 mg/kg) was the most effective, reducing operant responding by over 50% relative to the saline condition; whereas selective δ opioid receptor antagonist naltrindole disrupted performance only slightly at the highest dose (10 mg/kg). By contrast, selective κ opioid receptor antagonist nor-binaltorphimine had no effect irrespective of the dose administered. Thus, μ opioid receptor and to a lesser extent δ opioid receptor are involved in light seeking response. Nevertheless, the effects in [Sikora et al. \(2019\)](#) might not be specific to light reinforcers, as other studies reported that opioid receptor antagonists could also affect operant responding for appetitive reinforcers ([Hayward & Low, 2001](#); [Sakamoto et al., 2015](#)).

Cannabinoid receptors

Abnormalities in cannabinoid receptor signaling can also affect operant light seeking response. Unlike *Drd1a*, *Grm5*, and *Grm5^{D1}* mice ([Olsen et al., 2010](#); [Olsen & Winder, 2009](#); [Parkitna et al., 2013](#)), [Helfand et al. \(2017\)](#) reported that *Cnr1*-knockout mice lacking cannabinoid receptor CB1R had no difficulty in acquisition of operant light seeking responses under FR1. However, under more demanding ratio schedules (FR2 and FR4), these mice showed reduced operant light seeking. Moreover, under all FR schedules *Cnr1*-knockout mice collected fewer light reinforcers. By contrast, in *faah*-knockout mice with a deficiency in fatty acid amide hydrolase (FAAH)—thus lacking the primary degradative enzyme that hydrolyzes endocannabinoid anandamide—operant light seeking was enhanced, and more light reinforcers were collected by these mice compared to control animals under all FR schedules ([Helfand et al., 2017](#)). In general, the effect of cannabinoid receptor signaling deficiency is less severe than dopamine, glutamate, and opioid signaling deficiencies, suggesting that endocannabinoid signaling plays an indirect (*i.e.* modulatory) role in acquisition and expression of operant light seeking response.

Summary

Taken together, delivery of a light reinforcer that is contingent upon lever pressing or nose poking responses

can establish a persistent habit. The operant light seeking response (but not necessarily operant food seeking) requires D1R, mGluR5, as well as μ and δ opioid receptor signaling; it is also modulated by CB1R. Signaling *via* these receptors and their interactions (e.g., mGluR5–D1R) regulate the effectiveness of light as a reinforcing stimulus.

THE RELEVANCE OF LIGHT SELF-ADMINISTRATION TO DIGITAL TECHNOLOGY-BASED DISORDERS

Traditionally, animal models of psychiatric diseases are evaluated in terms of various validation criteria, such as face, construct, and predictive validity (*cf.* [Willner, 1984, 1986, 1990, 1997, 2016](#)). For example, *construct validity* is evaluated based on the similarity between the mechanisms driving the (mal)adaptive behavior in humans and the corresponding behavior in the animal model. In this respect, the mouse's persistent light seeking response on an operandum is behaviorally analogous to humans' habitual responding to sensory reinforcers of visual and non-visual modalities on digital devices. In humans, habitual responding to virtual rewards can be induced experimentally on digital devices. Prolonged training in a smartphone application-based game promotes participants' habitual responding with reduced sensitivity to virtual reward devaluation ([Gera et al., 2023](#)). Similarly, *overtraining* mice in an operant task with traditional food reward promotes habitual responding that is insensitive to food reward devaluation ([Bar Or & Klavir, 2021](#)).

Notably, in mice that are well trained in the operant light seeking task (under FR1), a relatively low dose of dopamine receptor antagonist causes *more* lever responding due to reduced salience of the light reinforcer (**see Dopamine receptors**). Thus, for mice that have acquired the instrumental contingency, their “urge” for sensory self-stimulation can be increased by limiting the intensity of the sensory reinforcer. A similar “frustration-like” effect can be found during the post-reinforcement period under fixed-interval (FI) schedules, where mice show bursts of lever-pressing response immediately after cessation of the light reinforcer ([S.K.E. Tam, D.M. Bannerman, & S.N. Peirson, unpublished data](#)). In humans, these compensatory mechanisms play a role in driving “addiction-like” behavioral responses to short-form videos on smartphone applications ([Tian et al., 2023](#)). Additional evidence of construct validity comes from findings reviewed in the previous section, which point to the fact that the key neurotransmitters and receptors involved in driving the mouse's operant light seeking behavior partially overlap with those involved in operant drug seeking behavior in humans and rodents (for review see [Koob & Volkow, 2016](#)).

Caveats of using the light self-administration paradigm

Although the light seeking paradigm provides a promising approach to examine the general mechanisms of (excessive)

light-induced habitual responding, it does not fully capture the complexity of digital technology-based disorders such as Internet-use disorders, which often arise from an interplay of factors that go beyond sensory self-administration. While artificial light may partially strengthen habitual responding on digital devices *via* various mechanisms (see **Non-visual effects of light: Its incentive value and hedonic property**), it is unlikely to be the sole or dominant factor. Unlike substance addiction, in which an addictive drug leads to chronic neuroplastic changes (Everitt & Robbins, 2005, 2016; Koob & Volkow, 2016), behavioral addictions are unlikely to exert such a rapid and powerful effect on the brain (e.g., Clark, Boileau, & Zack, 2019), and Internet addiction is more related to cognitive, affective, and social factors such as cognitive stimulation, information seeking, and social validation (Brand et al., 2016, 2019).

Other existing animal models

An existing model for behavioral addiction is the rodent gambling task, in which food-restricted rats are required to discriminate among multiple operanda with different reward sizes and different penalties (i.e. reward omission) after food delivery. In the typical version of the task, responding to the operandum that leads to a larger immediate food reward is followed by a longer period of reward omission and is therefore suboptimal in the long run. Rats tend to avoid this suboptimal choice; instead, they show a preference for the alternative operandum that leads to a smaller immediate reward but with less reward omission (Rivalan, Ahmed, & Dellu-Hagedorn, 2009; Zeeb et al., 2009). Operant performance in this task is sensitive to pharmacological (serotonin receptor agonists and dopamine receptor antagonists), brain (prelimbic, orbitofrontal, and cingulate cortical lesions), and environmental manipulations (de Visser et al., 2011; Kim et al., 2017; Pais-Vieira et al., 2007; Rivalan et al., 2011; Zeeb et al., 2009). Compared with the light seeking task, the gambling task is procedurally more complex; animals are often given ≥ 4 choices in the operant chamber, and the task assesses the extent to which animals are willing to take risk and respond persistently on a suboptimal choice—this cannot be examined by using the light seeking task as presented in Fig. 1 (top panel). However, it remains to be determined whether light reinforcers can be as effective as food reinforcers to support optimal decision making in rodents. If this is the case, it may be possible to combine different paradigms and examine multiple behavioral phenotypes in a unified manner. Finally, other paradigms to study suboptimal choice behavior relevant to gambling disorder has also been developed in other species, such as in pigeons (Zentall, 2023).

CONCLUSION AND OUTLOOK

Taken together, these findings indicate that mouse models employing light as reinforcers may build the basis for associative learning models in animal studies aiming to

understand the general mechanisms underlying digital technology-based disorders. By using the mouse operant light seeking paradigm, we may ask a wider range of questions (Table 1) related to the underlying biological mechanisms of maladaptive habit formation related to the use of digital devices. More specifically, the paradigm may allow us to disentangle the relative contributions of biological (e.g., biological age, sexual dimorphism, or genetic polymorphism) and environmental factors (e.g., boredom or environmental enrichment) in determining an animal's predisposition to excessive operant light seeking. For example, can polymorphism of the endocannabinoid-degrading enzyme gene *faah*—which is associated with substance misuse in humans (Sipe, Chiang, Gerber, Beutler, & Cravatt, 2002)—enhance self-administration of sensory stimulation on digital devices, partly mimicking the enhanced light self-administration phenotype of *faah*-deficient mice (Helfand et al., 2017; see **Cannabinoid receptors**)? The light seeking paradigm may also allow us to precisely dissect the underlying neurobiological adaptations that accompany the transition from volitional to habitual use and may ultimately allow to determine common and distinct mechanisms that underlie substance *versus* behavioral addictions (Olsen et al., 2010; Olsen & Winder, 2009). Finally, these animal models may allow us to employ prospective and longitudinal designs to determine detrimental effects of modern-day maladaptive habits on the developing brain and long-term brain health (e.g., cognition, sleep/wake pattern, and circadian rhythm) which are ethically not possible in humans.

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