



Unconscious will as a neurobehavioral mechanism against adversity

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ABSTRACT

Incentive salience theory both explains the directional component of motivation (in terms of cue attraction or “wanting”) and its energetic component, as a function of the strength of cue attraction. This theory characterizes cue- and reward-triggered approach behavior. But it does not tell us how behavior can show enhanced vigor under reward uncertainty, when cues are inconsistent or resources hidden. Reinforcement theory is also ineffective in explaining enhanced vigor in case reward expectation is low or nil. This paper provides a neurobehavioral interpretation of effort in situations of adversity (which always include some uncertainty about outcomes) that is complementary to the attribution of incentive salience to environmental cues. It is argued that manageable environmental challenges activate an unconscious process of self-determination to achieve “wanted” actions. This unconscious process is referred to as incentive effort, which involves the hypothalamo-pituitary-adrenal (HPA) axis, noradrenaline, as well as striatal dopamine. Concretely, HPA-induced dopamine release would have the function to make effort—or effortful actions—“wanted” in a challenging context, in which the environmental cues are poorly predictive of reward—i.e., unattractive. Stress would only emerge in the presence of unmanageable challenges. It is hypothesized that incentive effort is the core psychological basis of will—and is, for this reason, termed “willing.”

1. Introduction

Motivational processes may appear simple in comparison with other psychological abilities such as reasoning and language. However, the attempts to uncover how they work have yielded considerable literature since the early 20th century, and important debates remain unsettled today. One of them, discussed in this paper, relates to the evidence that motivation has two behavioral effects difficult to reconcile within the same theoretical framework. First, motivation *directs* (or guides) behavior toward detected or expected rewards or reward cues (Flagel et al., 2011; Meyer et al., 2012; Robinson and Berridge, 2013). For example, a vulture will follow the smell of a carcass in the savanna or will expect future meal due to the presence of predators hunting nearby. Second, motivation *boosts* (or energizes) behavior under conditions of reward uncertainty, compared to conditions in which rewards are abundant or, at least, predictable. For example, a rat exposed to an inconsistent reward-predictive cue will interact more vigorously with the cue (Anselme et al., 2013; see also Bateson et al., 2021) or will explore more locations before visiting the cued food area (Stahlman and

Blaisdell, 2011). These two aspects create a paradox because, if motivation guides behavior toward reward cues, the effort invested should be proportional to reward probability rather than amplified when reward probability is lower.

In this paper, I argue that this paradox vanishes if we consider that the directional and the uncertainty-related energetic components of motivation represent distinct, though related, core psychological processes. The former process is motivational attraction and is referred to as incentive salience or “wanting,” which can be measured as approach behavior to cues predictive of reward or to the reward itself (Berridge and Robinson, 1998). Incentive salience theory posits that incentivization of external cues is mostly dependent on dopamine release in the ventral striatum (Berridge and Robinson, 1998). This process might be the unconscious underpinning of desire (Anselme and Robinson, 2016; File et al., 2024; Toates, 2014). The second process is only partly related to “wanting” and would be at the origin of self-determined effort, induced by moderate activation of the hypothalamo-pituitary-adrenal (HPA) axis in interaction with noradrenaline (see Table 1 for more details). These two aspects work in concert in the form of HPA-induced

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Table 1
Main phenomena and their characterization.

Phenomena	Definition and brain mechanism
<i>Incentive salience</i> (or “wanting”)	Transformation of ordinary cues in potent incentives (cues or rewards) leading to approach behavior. The incentives are unconsciously “wanted” (no challenge required). Brain mechanism: Striatal dopamine release.
<i>Stress</i>	Negative emotional state resulting from prolonged exposure to an unmanageable challenge and compromising wellbeing. Brain mechanism: High (deleterious) activation of the HPA axis.
<i>Incentive effort</i> (or “willing”)	Self-determination to achieve “wanted” actions, leading to behavioral overinvestment in the presence of reward cues of low predictive value (reward uncertainty) to meet a manageable challenge. Resolving uncertainty is unconsciously “willed.” Brain mechanism: HPA-induced dopamine release.
<i>Self-determination</i>	Preparation for action in a context of manageable challenge (reward uncertainty). It is a major part of incentive effort, that is, the process that prepares organisms to resolve uncertainty. Brain mechanism: Moderate (salvatory) activation of the HPA axis, in interaction with noradrenaline release.
“Wanted” action	Action imbued with incentive salience. An action can be “wanted” because of (a) the presence of “wanted” cues or rewards in the environment (motivational attraction), in which case no self-determination is involved, or (b) a self-determination to meet an environmental challenge (reward uncertainty), irrespective of the reward value to be expected. Brain mechanism: Striatal dopamine release (with or without HPA activation)
<i>Environmental challenge</i>	Uncertainty about a “wanted” outcome. The challenge itself is not “wanted,” so trying to meet it requires that organisms are “willing” to invest time and energy for an unguaranteed outcome.

dopamine release and are referred to as incentive effort¹ (Anselme, 2023). It is measured as behavioral overinvestment in the presence of reward cues of low predictive value—compared to reward cues of higher predictive value. Incentive effort is assumed to have evolved because this mechanism made a number of environmental challenges manageable and it will be distinguished from stress—which also recruits the HPA axis—as a negative emotion that compromises wellbeing (see Table 1). Here, it is carefully hypothesized that incentive effort is the unconscious underpinning of will, and is for this reason called “willing”—for consistency with “wanting.”

The former theories of motivation already recognized that multiple aspects of motivational phenomena had to be explained, in particular their ability to provide behavior with a direction and some energy (e.g., Beck, 1978; Duffy, 1951; Hull, 1943; Tinbergen, 1951; Young, 1961). However, the dominant concept of drive at that time was mostly focused on the energetic component: Organisms have needs to be satisfied and need-related internal drives fuel their behavior to reduce those needs. There was no clear specification of where an animal had to go to satisfy a need once its behavior was energized—a problem particularly striking when all possible behaviors were supposed to depend on the activation of a single, general drive (e.g., Hull, 1943). With a general drive, any drive-cue habit (e.g., hunger-fridge) is lost among thousands of other

¹ This process was initially referred to as incentive hope (Anselme, 2015a), meaning that animals exposed to uncertain rewards invest more effort in the task because they behave as if they hoped for consistent CS-reward pairings. This concept was mostly developed to account for the enhanced behavioral effects under partial reinforcement in Pavlovian autoshaping. However, “hope” as an as-if concept is not a process; it is therefore difficult to distinguish from the process of incentive salience and seems to involve an irreducible cognitive layer of goal-directedness that is undesirable in this context (see further, in text). In addition, the question of CS-reward consistency should likely be treated separately from that of effort (Anselme, 2023). In comparison, the notion of incentive effort is more descriptive and attributes incentive properties to effort or effortful actions rather than to cues or rewards, allowing effort-related incentive properties to be distinguished from cue- or reward-related incentive properties (see further, in text). Beyond these considerations and refinements, the earlier developments remain applicable.

drive-cue habits involving the same drive, so that any decision to act is subjected to a combinatorial explosion of possibilities. In addition, organisms have no opportunity to satisfy a drive (whether general or specific) in a novel environment, given the absence of familiar cues allowing the selection of relevant drive-cue habits. The question of reward uncertainty was also poorly discussed, except in the context of a frustrative event—i.e., unexpected reward omission—presumably responsible for behavior invigoration (Amsel, 1958). Drive theory was an intuitive way to explain how behavior can be energized, but it has been refuted by a number of findings and is no longer considered a valid description of how motivational processes work—due to space limitation, these findings cannot be reported here (for reviews, see Anselme and Robinson, 2016; Berridge, 2004, 2018).

Drive theory and its mysterious internal energy principle (Hinde, 1970) was gradually replaced by incentive interpretations of motivational phenomena, which suggest that behavior is rather incentivized by external cues whose perception or recall may, under some circumstances, activate the brain reward circuit (Bindra, 1978; Toates, 1986; Berridge and Robinson, 1998). For example, hunger makes food more appetizing, lights and sounds in casinos make slot machines more attractive, and loneliness or social events increase the temptation of consuming alcohol or other drugs. Incentive views easily account for the directional component of behavior: Organisms become attracted by some stimuli and hence approach them or the location where they are expected. Additionally, incentive salience theory can also explain the energetic component of motivation to some extent, depending on the strength of dopamine-induced stimulus “wanting.” As already noted, however, this process does not tell us how reward uncertainty can boost behavior. No better explanation is to be found with instrumental conditioning because, as an expectation-based process, it should consistently reduce response vigor instead of increasing it under reward uncertainty.

Incentive effort may account for the boosting behavioral effects of reward uncertainty in a way that complements incentive salience (Anselme, 2023). The word “effort” means more investment in a task, and effort may take various forms such as a greater intensity of a response, more time spent in a task, or even a higher variability in the elicited response—because varying a behavioral pattern is likely to require more physical/cognitive resources than displaying a fixed action pattern. The word “incentive” means, like with incentive salience, that this process is both unconscious and incited. Incentive effort is assumed to motivate investment in a task involving unguaranteed rewards, especially when uncertainty is unavoidable (more challenging). In other words, uncertain rewards are poorly “wanted”—e.g., animals and humans typically prefer reliable over unreliable reward cues (e.g., de Jonge et al., 2008; Eisenreich et al., 2019; Gneezy et al., 2006; Kahneman and Tversky, 1979). But they may render effort incentive on its own to boost responding, promote exploratory search, and possibly resolve uncertainty (Anselme, 2023; Anselme and Hidi, 2024). This view is consistent with incentive salience theory, and not a return to drive theory or an amendment of frustration theory (Anselme, 2022). The concept of incentive effort aims to bring the missing piece that provides an integrative interpretation of the incentive motivation process: Incentivized behavior is guided by cues in the vicinity and boosted (strengthened, lengthened, and randomized) by a challenging context of uncertainty to be resolved.

2. Incentive salience as the directional component of incentive motivation

This section describes how the process of incentive salience attribution to cues and rewards works. Let us start with a classic example: Pavlovian autoshaping. In this experimental procedure, a rat is exposed to multiple trials that consist of the sudden insertion of a lever (conditioned stimulus or CS) from a wall in a Skinner box. In each trial, retraction of the lever CS a few seconds later is followed by food delivery

(unconditioned stimulus). After repeated lever-food association, the lever is therefore learned as a predictor of food delivery—no specific behavior or dopamine burst occurs if the lever-food temporal pairing is random (Garr et al., 2024; Rescorla, 1968). With consistent lever-food pairings, however, the behavior observed during lever insertion may differ across rats: Some individuals (goal-trackers) approach and interact with the food magazine, while others (sign-trackers) approach and interact with the lever. In other words, the lever becomes motivationally attractive for sign-tracker rats only (e.g., Meyer et al., 2012). Interestingly, in this procedure, the lever is approached by sign-trackers despite no action being required to obtain food and despite the food being delivered in a different location. Thus, among sign-trackers, the incentive salience of the food is somehow transferred to the lever CS, transforming this neutral cue in something both psychologically salient and incentive—i.e., “wanted” like food itself (Berridge, 2007; Flagel et al., 2007).

2.1. Incentive salience is proportional to reward probability

The reward circuit involves several brain regions and neurotransmitters (Ikemoto, 2010) and incentive salience attribution to cues through mesolimbic dopamine release is one of its major products (e.g., Pecina et al., 2003; Saunders and Robinson, 2012). This process operates without any cognitive or conscious control of the decision to approach a CS. The gradual transfer of incentive salience from the food to the CS fits well the evidence that, after completion of a learned CS-reward association, dopamine release occurs at the CS onset and becomes lower at the time of reward delivery (Anselme, 2013; Berridge, 2012)—although other interpretations related to associative learning, not discussed here, have been provided (e.g., Daw and Doya, 2006; Schultz, 1998). If dopamine codes reward value, the transfer should therefore be more effective (faster and more complete) if the CS is 100% rather than, say, 50% predictive of the reward. With a 100% probability, there is indeed no opportunity to miss and hence inhibit motivational transfer from the reward to the CS. Thus, *the transfer of incentive salience from the reward to the CS must be proportional to the consistency of the CS-reward association*².

This point is crucial to understand incentive salience as the directional component of incentive motivation through approach behavior. If a more consistent CS-reward association induces a higher attribution of incentive salience to the CS because motivational transfer from the reward to the CS is more effective, then, a CS with a higher predictive value is more likely to be approached—learning facilitation may indirectly speed up motivational transfer. Also, a higher reward probability following the CS presentation reduces spatial and temporal variability in the responses to the CS (Blaisdell et al., 2016), indicating narrower cue-triggered motivational focus. This fact advocates for a major role of incentive salience in a more effective approach to familiar stimuli or locations previously associated with reward. In contrast, a lower reward probability degrades the process of incentive salience attribution and approach behavior while favoring more variable responses and the exploration of other options. For example, in an open field, Stahlman and Blaisdell (2011) placed sixteen cups containing sand, surmounted by small wood blocks with two different landmarks. When rats were exposed to the high-food landmark, the cued cup was baited 100% of the time with a food item buried in sand, and this probability was only 20% with the low-food landmark. Rats showed more variability in total number of cups inspected before searching in the cued cup with the

² This idea does not contradict the evidence that the incentive property of a stimulus occurs independently of its predictive value (e.g., Flagel et al., 2007). After all, the distinction between incentive and predictive effects (sign- vs. goal-tracking) has been established in rats using a lever CS 100% predictive of reward delivery. Here, my point is this: Among sign-trackers, the theory predicts that the transfer of incentive salience from the reward to the CS will be higher if reward probability is higher.

low-food landmark than with the high-food landmark. This variability effect is indicative of incentive salience degradation when reward probability decreases, causing exploratory search rather than resource exploitation through focused approach behavior (Anselme, 2023).

2.2. “Wanted” actions and the problem of challenging uncertainty

I have suggested that the effectiveness of the transfer of incentive salience from the reward to the CS is proportional to the probability of reward, which seems to make approach behavior more focused. But transfer effectiveness is also a function of the appetitive value of the reward. Thus, a detected or expected CS is more likely to be approached if it is associated with an appetitive reward. In this respect, incentive salience says something about behavior vigor, because an appetizing food should be approached faster and with greater effort than ordinary food (Fig. 1A). To use a classic analogy (Berridge, 2007), it is like saying that a strong magnet (appetizing food) will attract iron (the organism) with a higher strength than a weaker magnet (ordinary food). This is how incentive salience theory accounts for the energetic component of incentive motivation, and there are no doubts that this process operates in a number of situations. However, whether such an explanation of behavioral invigoration can be generalized to situations in which the organism encounters a difficulty to be overcome is questionable (Fig. 1B). A difficulty may occur in multiple contexts of unguaranteed (uncertain) outcome, where consistent conditioned cues to which to react cannot easily be identified. An unguaranteed outcome may have a probability significantly lower than 100% and should therefore decrease incentive salience attribution to its predictive cues. For example, the absence of food at a cache or the invasion of a burrow by ants require an animal some effort to find another meal or shelter, but incentive salience is unlikely to be directly involved in the management of such difficulties. Even if finding another food source or another burrow is “wanted,” the animal may have no clues capable of directing its behavior in the short term. Where does the extra energy required to meet the challenge come from?

After Robinson and Berridge (2025), incentive salience is not only attributed to rewards and their predictive cues, but also possibly to actions. There is indeed no reason why incentive salience would not imbue actions. For example, people with a drug addiction may feel an urge to get in touch with their dealer to obtain some drug. Nevertheless, this process follows the same logic: Cues and rewards guide actions, whether they are physically present or mentally represented. People with addiction are motivated to use behavioral strategies they know to be effective in obtaining what they “want.” Thus, an urge to act should also be proportional to the probability—not the uncertainty—of a reward. It does not result from a self-determination to counter uncertainty. People have numerous wishes and phantasms they do not try to satisfy, suggesting that self-determination—whether uncertainty is present or not—is actually not a defining property of “wanting” and desire. For example, rats repeatedly exposed to a lever CS that predicts the delivery of salt water in their mouth, attempt to go away from it when presented (Robinson and Berridge, 2013). But after inducing brain signals of salt deprivation in those rats, without additional training, the lever CS becomes instantly attractive. The approach behavior of the initially “unwanted” lever may be imbued with incentive salience but its attraction is entirely controlled by the rewarding value that salt water now represents for the rats. A more extreme situation occurs following the optogenetic stimulation of the central nucleus of the amygdala, immediately after an aversive shock rod has been accidentally touched by rats (Warlow et al., 2020). This brain stimulation induces a surge of incentive salience to the point that the rats then touch and even chew the shock rod repeatedly, climbing a large opaque block (obstacle) to reach it. Thus, the shock rod is just irresistible despite being strongly aversive and avoided otherwise—i.e., costly for the rats. For this reason, even if approaching the rod is imbued with incentive salience, it could probably be not described as self-determined. An action is more likely to be

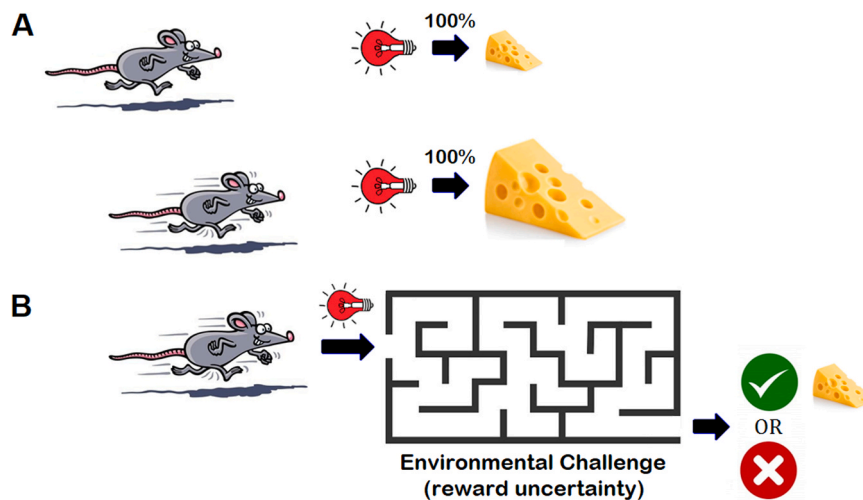


Fig. 1. A: A small reward (piece of cheese) causes moderate approach behavior to external cues (light bulb) compared to a larger reward, explaining both the directional component of behavior and the difference in response strength—all other things (such as food deprivation level and food probability) being equal. B: Response strength may be enhanced by an environmental challenge (outcome uncertainty), as it is with a larger (vs. smaller) reward. But the incentive salience attributed to external cues in a challenging context is unlikely to account for this effect, because the attribution process should be reduced when compared to an unchallenging context of guaranteed reward.

recognized as self-determined (or even voluntary) if some effort is being produced despite unguaranteed reward, suggesting that the effort is primarily incentivized by uncertainty resolution rather than by the cued reward itself (Anselme, 2023; Anselme and Hidi, 2024). In Warlow et al.'s (2020) experiment, an uncertain brain stimulation after touching the shock rod would probably decrease the rats' performance due to the risk (high cost) of touching the rod without receiving any brain stimulation—those rats “want” the reward, they are not self-determined to resolve reward uncertainty.

3. Uncertainty processing is an incentive phenomenon

In Pavlovian conditioning, cues (and actions) are attributed with incentive salience despite having no positive or negative consequences for the individual—c.f., autoshaping. Instrumental conditioning is quite the opposite: It is insensitive to cue attraction and a function of the expected consequences about reward. Thereby, one major theoretical foundation of instrumental conditioning is the law of effect (Thorndike, 1911), which suggests that animals would repeat profitable actions and give up harmful/useless actions. Another important theoretical framework is the matching law (Herrnstein, 1961), which predicts that animals would distribute their activity proportionally to the profitability of the available options. Thus, reward expectation is the driving force of instrumental conditioning—what Skinner (1981) called “selection [of action] by consequences.”

Interpreting the stimulating behavioral effects of reward uncertainty through instrumental conditioning leads to two major problems. First, we know that conditioned cues induce a release of mesolimbic dopamine and that this effect is amplified with cues predictive of uncertain rewards (Bjork and Hommer, 2007; Dreher et al., 2006; Fiorillo et al., 2003; Hart et al., 2015; Linnert et al., 2012; Preuschoff et al., 2006; Zack et al., 2014). However, dopamine does not seem to play a significant role in many instrumental conditioning preparations (Dickinson et al., 2000; Fraser et al., 2023; Koch and Hans-Ulrich Schnitzler, 2000; Lex and Hauber, 2010; Sicre et al., 2020; Wassum et al., 2011). Very often, dopamine released during instrumental behavior is associated with exertion of effort (e.g., Salamone et al., 1994, 2007; Salamone and Correa, 2012), sometimes in the presence of some forms of uncertainty (e.g., Beeler et al., 2010). But effort production and the conditions in which it has to be produced, seem to matter more than the instrumental nature of the task. In an instrumental context, uncertain rewards require

more effort to be obtained and dopaminergic effects are found but, surprisingly, they do not always transpire in the instrumental actions. Mascia et al. (2019) pre-exposed rats to a variable-ratio or a fixed-ratio schedule for saccharin (55 sessions)—the responses being measured as lever presses. The variable ratio (VR20, 1–39 responses randomly required) induced a form of uncertainty that strongly boosted dopamine release relative to the fixed ratio (FR20), but the rats' responses to the VR and FR schedules were similar (see also Singer et al., 2012). It is only when the rats were exposed to an open field (where no instrumental action was possible) under an amphetamine challenge that dopamine revealed its behavioral effects—with VR rats running a longer distance than FR rats. Interestingly, adding a cue to a VR/FR training also reveals the effects of reward uncertainty on lever pressing. Robinson et al. (2023) used water and sucrose as rewards with a low-range variable-ratio schedule (VR3, 1–6 responses randomly required) or a fixed-ratio schedule (FR3), both followed by a light-tone compound stimulus acting as a CS without consequences. Rats pressed the lever more during the light-tone compound stimulus in the VR3 than in the FR3 group, despite no differential responses to water or sucrose prior to introducing the compound stimulus. Thus, the enhanced dopaminergic effects observed following uncertainty training in instrumental conditioning suggest the involvement of an incentive process: They do not influence behavior per se, except if the individuals have the opportunity to encounter non-instrumental cues.

Second, I showed earlier why reward uncertainty in Pavlovian tasks should diminish the transferability of incentive salience from the reward to the CS, compared to reward certainty. The law of effect and the matching law also predict a negative effect of reward uncertainty on instrumental performance, because uncertainty reduces reward expectation and should therefore generate a lower investment than a more consistent option. The examples above suggest that instrumental conditioning is unaltered by uncertainty, indicating a possible violation of those laws by other processes in these experiments (e.g., McDowell, 2013). However, in order to illustrate the decrease in performance under reward uncertainty, I would like to consider goal-tracking behavior. Goal-trackers do not attribute incentive salience to discrete cues but instead become attracted by the food dish... unless it is also by the reward. Indeed, although they do not produce more dopamine, with a consistent CS, their conditioned responses are as vigorous as those of sign-trackers. If cue valuation fails to explain their vigorous responses, it is possibly because goal-tracking is mostly instrumental rather than

Pavlovian (Pellón et al., 2018; Strand et al., 2022; but see Darvas et al., 2014; DiFeliceantonio and Berridge, 2012). Several findings support the instrumental nature of goal-tracking, in that this behavior is more sensitive to an alteration of the reward delivery conditions in extinction (Ahrens et al., 2016) and after punishment (Pellón et al., 2018) than sign-tracking. Also, approaching the food dish, but not the lever CS, correlates positively with the palatability of the reward (Patitucci et al., 2016) and negatively with reward devaluation, whether induced by satiation (Patitucci et al., 2016) or by pairing the reward with illness (Morrison et al., 2015). Accordingly, it has been shown that goal-trackers decrease their responses under reward uncertainty, as predicted by reinforcement theories (Gottlieb, 2005; Harris, 2011; Harris and Carpenter, 2011; Navarro et al., 2024). Whether goal-tracking is fully instrumental or not is unimportant here, but it seems processed differently from sign-tracking (Iliescu et al., 2018; Morrison et al., 2015) and in accordance with the rules based on reward expectation.

In short, neither incentive salience (Section 2) nor instrumental expectations (Section 3) can account for the enhanced responses typically observed under reward uncertainty. This suggests that the invigoration of lever pressing with an inconsistent CS in sign-trackers depend on another process, whose incentive effects add to those of incentive salience in Pavlovian autoshaping. The nature of this process will be discussed in the next section.

4. Incentive effort as the missing energetic component of incentive motivation

From this section, it is argued that an organism's reactivity to situations in which reward predictability is low or nil requires an incentive process independent of cue salience or reward expectation but instead related to effort production. This process, called incentive effort, is assumed to be the energetic component that operates in response to unpredictable reward encounters to compensate for the lack of cognitive control and maximize the chance of success. Its function is not to facilitate approach behavior through cue or reward "wanting" (directional component) but to stimulate, lengthen, and randomize behavior to meet environmental challenges. Incentive effort can be defined as the self-determination to achieve a "wanted" action (energetic component) and may represent the core psychological process of will—for this reason, it is referred to as "willing"³ (see Table 1). Self-determination is a crucial property of "willing" (just as it is of will), since it denotes the process that prepares organisms to face an environmental challenge, and it consists of the activation of the HPA axis in interaction with noradrenaline. It was shown that "wanted" actions may result from incentive salience in the absence of self-determination, in which case organisms become attracted by cues and rewards through dopamine release. Environmental challenges play no role in this process. In contrast, "wanted" actions may also result from self-determination, through HPA-induced dopamine release, leading organisms to behave irrespective of cues and rewards but rather in response to challenging events. Thus, "willing" (incentive effort) and "wanting" (incentive salience) are both unconsciously processed by the brain, but they respectively differ by the presence or absence of self-determination.

A compelling example of incentive effort is contrafreeloading, a form of exploratory behavior where animals prefer to seek unguaranteed food rather than consuming the same food available in abundance. For example, gerbils (*Meriones unguiculatus*) choose to spend more time searching and eating sunflower seeds from a bowl containing 200 items hidden in sand despite the presence of another bowl containing 1000 sunflower seeds without sand (Forkman, 1991, 1993). No incentive cues

can attract their behavior to the 200-seed bowl, given that the expectation of sunflower seeds in this bowl is much lower and that a bowl of sand without seeds is poorly attractive to gerbils. Many factors influence contrafreeloading, which optimally occurs when food deprivation is low and the required effort to get food remains moderate (Inglis et al., 1997). Nevertheless, the preference for earned over free food has not received any clear psychobiological explanation yet—beyond evolutionary (ultimate) considerations suggesting that, for survival reasons, animals try to be continuously updated through exploration about possible significant changes in reward rate in the vicinity (but see Frederick and Cocuzzo, 2017; Milella et al., 2008; Schepisi et al., 2016). This behavior has been identified in many animal species (Inglis et al., 1997) and is directly related to the question of challenging uncertainty: Animals decide to freeloading when the situation is no longer uncertain (e.g., Bean et al., 1999; Forkman, 1996; Havelka, 1956).

The effort deployed by an individual to explore a novel environment is likely to come with the detection of familiar cues (stones, trees, bird songs, etc.) and the expectation of specific events (females, shelters, predators, etc.) capable of modulating incentive salience. In this context, incentive salience would attract the individual towards the most attractive cues, a strategy that favors resource exploitation (Fig. 2, left). In contrast, incentive effort would enhance curiosity and a propensity to invest time and energy in poorer areas, a strategy that favors exploratory search (Fig. 2, right). Of course, the propensity to explore or contrafreeload may vary (e.g., Andrews et al., 2015; Anselme et al., 2018; Forkman, 1996), depending on whether the task is challenging or not, and perhaps whether it is a source of insecurity—which might inhibit curiosity. But there is evidence that rats continue to sample locations with contaminated food (Inglis and Shepherd, 1994) or associated with nausea—after receiving an injection of lithium chloride, a malaise-inducing substance that makes the paired food items subsequently avoided (Melcer and Timberlake, 1985). Also, across younger and older human participants, it was found that uncertainty enhances exploration when the outcomes are expected to be negative, but not when they are expected to be positive or neutral (Yagi et al., 2023). Incentive effort might be systematic under challenging uncertainty and may sometimes show its behavioral effects in unexpected ways. For example, pigeons spent more time, produced more pecking effort, and visited more often the area of a board in which hidden food items were predictable in each hole of the board at the beginning of a session, compared with an adjacent area where the food items were randomly distributed in only one third of the holes (Anselme et al., 2022, 2024). However, per visit, the pigeons spent more time and produced more effort in the random area—even when the number of food items available varied positively or negatively from day to day relative to their fixed number in the predictable area (Anselme et al., 2024). The higher

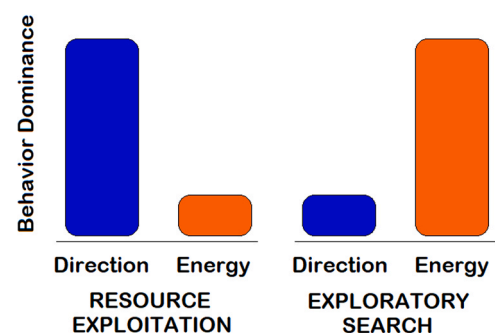


Fig. 2. Double dissociation between the directional and energetic components of incentive motivation. During resource exploitation, behavior is mostly directed to significant cues through incentive salience ("wanting"). The animal attempts to approach those cues. During exploratory search, especially in the absence of significant appetitive cues, behavior is mostly energized through incentive effort ("willing"). The animal attempts to meet the uncertainty-induced challenge. Both processes are not mutually exclusive.

³ Contrary to will, "willing" is an unconscious process and does not therefore include any kind of introspective Self—the word "self" only refers to the organismic rather than environmental origin of determination.

performance per visit in the area of lower food density is at odds with the predictions of incentive salience theory or the matching law, but fits well the prediction of the incentive effort hypothesis.

Recruiting incentive effort in unchallenging environments is useless. If incentive effort occurs in relatively hostile environments, it is presumably because, as a result of natural selection, this strategy made some unavoidable challenges manageable. Struggling against the encountered difficulties (by means of more effort deployed, more time spent, and/or greater behavioral variability) is simply more beneficial for survival than developing stress and focusing on outcome insecurity (Anselme and Hidi, 2024). For example, Griffin et al. (2014) studied problem solving in the common myna (*Sturnus tristis*) and found that a greater diversity in motor actions (more beak, head, and feet movements) allowed the birds to show more variations in their contacts with objects and hence to increase the probability of solving a problem—such as opening a compartment with food inside. In this study, perseverance was positively correlated with engagement in the task but was not sufficient to achieve it. In line with this, low confidence in what to believe was shown to favor curiosity (Cohanpour et al., 2024) and exploration (Boldt et al., 2019). Perhaps in the same vein, low confidence may also lead people to pay for a better confidence level (Eliaz and Schotter, 2010; Rodriguez Cabrero et al., 2019) and nonhuman animals to choose to the detriment of reward procurement (Plate et al., 2023; Vasconcelos et al., 2015). Contrary to a widespread idea, effort is not always perceived as a cost that organisms tend to avoid (Anselme and Hidi, 2024). People and Rhesus monkeys were found to exert cognitive effort in tasks from which they expected no additional external reward (Clay et al., 2022; Harlow, 1950; Lin et al., 2023), so that effort necessarily gains its incentive value from other sources.

Behaviors compatible with incentive effort have also been identified in two woodlice species, *Porcellio scaber* (Anselme, 2015b) and *Armadillidium vulgare* (Anselme et al., 2023). The woodlice showed more rearing-up behaviors on the walls of a compartment without reward when they were exposed to random visual patterns on the walls (black and white squares) and random tactile patterns on the floor (gained and smooth pieces of paper), compared to regular patterns (alternation of black and white strips on the walls and of gained and smooth strips on the floor). Those cues had never been associated with reward, so they had no conditioned value. But the woodlice might have perceived the random environment as more challenging than the regular environment, because “when the environment is more random, failing to escape after exploring a part of it does not inform about the inability to escape elsewhere in the apparatus, as the visuo-tactile configurations are different” (Anselme et al., 2023, p. 2). For sure, the neurobiological mechanism of incentive effort is different in invertebrates compared to vertebrates. Nevertheless, biochemical equivalents may exist—in crustaceans, a zoological group that includes woodlice, responses to environmental challenges seem to involve the hyperglycemic hormone and octopamine (Fehsenfeld et al., 2023), which are functionally similar to glucocorticoids and dopamine in vertebrates, respectively. In the next section, I examine the presumed neurobehavioral bases of the self-determination of “wanted” actions in vertebrates.

5. The presumed psychobiology of incentive effort

We now have to understand why incentive effort differs from incentive salience and how self-determination relates to “wanted” actions. The psychobiology of will remains poorly investigated, except in the context of free will (e.g., Hallett, 2007; Sapolsky, 2024), and this section presents what the unconscious psychobiological origins of will could be. I hypothesize that the psychobiological basis of incentive effort consists of a neurobiological pathway that comprises noradrenaline, glucocorticoids, and dopamine. First, the interaction between noradrenaline and glucocorticoids may explain self-determination as a preparation for action in a challenging context (Sections 5.1 and 5.2)—a process to be distinguished from intention (Section 6). Second,

glucocorticoid-induced dopamine release may explain how the prepared action acquires a motivational value (the action becomes “wanted”), despite an absence of cues reliably predictive of reward in the environment (Section 5.3).

5.1. Noradrenaline

There is strong evidence that noradrenergic neurons—especially in the locus coeruleus, in the brain stem—are necessary to energize behavior (e.g., Borderies et al., 2020; Jahn et al., 2018), among other effects on attention and cognitive flexibility (Arnsten and Li, 2005; Aston-Jones and Cohen, 2005; McGaughy et al., 2008). Noradrenaline does not control the incentive properties of reward cues but nevertheless plays a role in motivation, as its activation and the probability of producing a response increases with the size of an expected reward (Ventura et al., 2008; Bouret and Richmond, 2015). Many studies have discussed effort in tasks that could not properly separate its neurobehavioral effects from those of the reward or reward cue to be approached (e.g., Salamone and Correa, 2002). However, such a separation is methodologically feasible and shows differences in brain activity (e.g., Croxson et al., 2009; Walton and Bouret, 2019).

For example, Varazzani et al. (2015) designed a task in which Rhesus monkeys were exposed to three sizes of reward (drops of water) and three levels of effort (squeezing a bar), associated and presented in a random order. Each combination of reward and effort was announced by a specific cue. If the monkeys were willing to obtain the reward, they had to produce the required amount of effort on the bar. The authors found that monkeys forwent the trials in which a high effort was required to obtain a small reward. They also found that the firing of dopaminergic neurons in the substantia nigra *pars compacta* preceded the decision of the monkeys to engage in the action or not and increased with the size of the expected reward. But the amount of physical force produced and pupil dilatation were both correlated with the firing of noradrenergic neurons in the locus coeruleus—i.e., noradrenaline seems necessary to mobilize resources and energize behavior.

In this task, reward delivery was contingent on the appropriate level of effort to be produced in a trial, and reward uncertainty might have increased with the imposed effort (Ang et al., 2015). The role of noradrenaline in uncertainty processing had already been discussed (e.g., Yu and Dayan, 2005). Jahn et al. (2018) suggest that noradrenaline might especially be important to face uncertain and dynamic environments, allowing animals to explore different options and adjust their actions to the present conditions. In humans, for example, Dubois et al. (2021) found that random exploration was attenuated by the noradrenergic antagonist propranolol but remained unchanged following the administration of the dopamine antagonist amisulpride. Also, Doren et al. (2023) found that reboxetine, a noradrenaline reuptake inhibitor, increased exploration in an optimal foraging task with humans: Compared to the placebo group, the individuals in the reboxetine group reduced residency time in all patches and left those patches despite remaining higher reward rates. These exploratory effects did not occur in individuals acting under methylphenidate, a dopamine reuptake inhibitor. As a challenge, reward uncertainty requires a significant mobilization of energy to act and might therefore recruits noradrenergic neurons (Bouret and Richmond, 2015). It was indeed found that the extra amount of energy required to trigger an action—and reflected by the activity of locus coeruleus neurons—is inversely related to the amount of energy deployed at a cue: “[T]he greater the incentive, the less energy would be needed at the time of the action to reach the threshold and trigger the response. [...] This is analogous to the subjective effort required to act when the expected reward has little value: something must complement the objective reward value to perform the action” (Bouret and Richmond, 2015, p. 4012–4013). If the transfer of incentive salience from the reward to its predictive cue is reduced under reward uncertainty compared to reward certainty in Pavlovian autoshaping, as suggested earlier, I would predict stronger noradrenaline

release from the locus coeruleus when uncertainty is involved.

5.2. Glucocorticoids

Noradrenaline may be necessary to energize behavior, but it is unlikely to be enough to account for incentive effort or “willing” as defined earlier. Incentive effort requires a preparation for sustained, “wanted” action rather than acute energizing. A good candidate for this preparatory process is the hormonal cascade involving the HPA axis. Briefly, HPA activation starts with the production of corticotropin-releasing factor (CRF) in the hypothalamic paraventricular nucleus. In the anterior pituitary, CRF receptors stimulate the secretion of the adrenocorticotropic hormone (ACTH), released in the blood circulation. Its molecules bind to cells of the adrenal cortex, located atop kidneys, where glucocorticoids (cortisol, corticosterone) are produced. Finally, glucocorticoids exert negative feedback that downregulates the production of CRF and maintains homeostasis. The HPA axis strongly interacts with noradrenaline. On the one hand, noradrenaline partly controls HPA activation via the CRF (Dunn and Swiergiel, 2008). On the other hand, stimuli processed by the HPA axis reliably and robustly release noradrenaline (Sara and Bouret, 2012). The HPA axis is often believed to be specifically sensitive to aversive stimuli or events, and is, for this reason, referred to as the stress system. But there is now evidence that its function is vaster and that not all aversive situations induce HPA activation.

The valence (appetitive or aversive) of a stimulus does not really matter for HPA activation. Sexual behavior is highly rewarding and induces corticosterone levels as elevated as social defeat, which is highly aversive, in mice and rats (Koolhaas et al., 1997). Also, high- and low-ranking male baboons may show high glucocorticoid levels, despite being exposed to very different life conditions and stimulations—i.e., physical activity vs. social punishment, respectively (Archie et al., 2012). It is also worth noting that people show a strong raise in cortisol levels during sleep—between 4 and 8 am—in the absence of any appetitive or aversive state (Linkowski et al., 1993; Lovallo, 2006). This burst of cortisol at the end of the night is more likely to be necessary for the transition from sleep to wakefulness. In line with this interpretation, Dufty and Belthoff (1997) found that western screech-owls (*Otus kennicottii*), a nocturnal species, show a rhythm of corticosterone that is reversed relative to diurnal species. These examples, among many others, indicate that HPA activation denotes physiological arousal instead of stressful/undesirable experience (see also Jimeno et al., 2018; Koolhaas et al., 2011; Otovic and Hutchinson, 2015; Sapolsky et al., 2000; Villalba and Manteca, 2019). For example, being exposed to uncontrollable passive stimuli such as noise or pursuing a desired goal under well-controlled conditions does not cause HPA activation, contrary to a pursuit of the same goal when threatened (Dickerson and Kemeny, 2004). In their meta-analysis of 208 experiments, Dickerson and Kemeny (2004) showed that significant stimuli perceived as uncontrollable or situations involving potential criticisms by others increase cortisol levels in humans, although negative affective states do not have this ability per se. Indeed, when the conditions for action are uncontrollable, responses and outcomes may become dissociated and negative consequences cannot be avoided despite intense and repeated efforts. In these conditions, intense or prolonged HPA activation might be a signal for the brain that effort failed to meet a challenge, causing stress with possible negative consequences for wellbeing (Jensen and Toates, 1997). But HPA activation is clearly not a reliable correlate or predictor of stress, defined as a negative emotional state that compromises wellbeing and psychological health.

The relation between corticosterone/cortisol and a perceived challenge may explain, for example, the influence of early life stress on adulthood. Individuals that experience significant stress early in life, such as food and social deprivations, tend to become adults with enhanced abilities for exploration and resilience to stress (e.g., Andrews et al., 2015; Clinton et al., 2014; Monaghan and Haussmann, 2015;

Parker et al., 2007; Frankenhuys and Nettle, 2020). The episodes of stress have long-lasting behavioral effects, such as increasing take-off speed to the detriment of take-off angle in the starling *Sturnus vulgaris* (O’Hagan et al., 2015), and favoring impulsivity and risk-taking behavior in humans (Pepper and Nettle, 2017). Why? At a young age, when one’s survival is dependent on other individuals, any kind of challenge may be perceived as unmanageable and cause severe stress. This negative experience was shown to sensitize the HPA axis (e.g., van Bodegom et al., 2017). Later in life, when similar or other challenges are encountered, the HPA axis tends to respond at a higher level than normal to environmental stimulations, with various consequences including greater risk-taking, novelty-seeking, and creativity in humans (e.g., Pepper and Nettle, 2017; Robinson, 2010). Regarding creativity, “[p]eople who have experienced adversity may develop new ways of thinking in the hope that these new ways will lead to uncover more reliable signals for reward than strategies that appear to be more rational—such as focusing on one’s difficulties, saving money, etc.—but unable to eliminate adversity” (Anselme and Hidi, 2024, p. 5). Similarly, impulsivity appears to be an adjustment to harsh environmental conditions (Pepper and Nettle, 2017), perhaps aimed to reduce delays to potential rewards in a way that mimic the effects of enhanced effort to achieve a goal. If early life stress causes more investment in tasks associated with unguaranteed rewards while making individuals more resilient to stress later in life, this suggests that HPA overactivity contributes to meet manageable challenges in adulthood rather than being a response to stressful events.

A recent meta-analysis by Jimeno and Verhulst (2023) supports the view that HPA activation is strongly associated with the perception of a challenge to meet. They found that HPA activation positively correlates with metabolic rate—irrespective of the method used to elevate metabolic rate—more than exposure to aversive stressful stimuli. A challenge to meet—i.e., trying to counter the uncertainty about an outcome—is typically what motivates incentive effort. Could HPA activation simulate metabolic rate to prepare and sustain incentive effort in a challenging situation? Could this self-determination process be at the origin of “wanted” actions whose physiological effects are more likely to be positive than negative for the organisms? Before discussing this in Section 5.3, let me report a few examples showing that HPA activation has positive effects on physiological indicators of health and wellbeing (e.g., Sapolsky et al., 2000; Marasco et al., 2018; Reneerkens et al., 2002). Animals often look for a nonzero level of arousal. Hens show nest-building behaviors such as gathering and litter-placing even when the nest was pre-formed by the same individuals the day before (Hughes et al., 1989). This activity stimulates the HPA axis. Sows motivated for nest building have elevated cortisol levels (Lawrence et al., 1994), and an enriched environment increases HPA activation and wellbeing in captive mice and pigs—compared to standard housing (Beattie et al., 2000; Marashi et al., 2003; Wells, 2009). Overall, captive animals seem to be less stressed under temporary unpredictable rather than constantly predictable environmental and feeding conditions, developing fewer stereotypies and more exploratory behaviors (Bassett and Buchanan-Smith, 2007; Bloomsmit and Lambeth, 1995; Shepherdson et al., 1993). Similar salvatory effects of HPA activation on wellbeing have also been reported in humans after episodes of video gaming (Aliyari et al., 2019; Pallavicini et al., 2018; Porter and Goolkasian, 2019), and a higher trait anxiety was even associated with diurnal decline in salivary cortisol in pregnant women (Kivlighan et al., 2008). Incentive effort is assumed to require HPA activation to trigger and sustain effortful investment in challenging situations, and should therefore play a major role in stimulating contexts of reproduction, parental care, food search, migration, and other behaviors (e.g., Angelier et al., 2007; Crossin et al., 2012; Jessop et al., 2002; Love et al., 2014; Pravosudov, 2003).

5.3. Glucocorticoid-induced dopamine release

The energy component of motivation, presumably mediated by noradrenaline and glucocorticoids in challenging situations, has been presented as controlling self-determination. Explaining how self-determination may lead to “wanted” actions is now necessary—a vigorous “wanted” action that requires both self-determination and a challenging context of poor reward cues should not be the effect of “magnetic” attraction by cues or reward expectation. Here, I argue that self-determination leads to “wanted” actions in challenging situations through glucocorticoid-induced dopamine release (Fig. 3).

Reward uncertainty is at the heart of any kind of challenge, and there is overwhelming evidence that repeated exposure to reward uncertainty not only does stimulate behavioral investment (e.g., Anselme et al., 2013; Ruggeri et al., 2023; Stahlman and Blaisdell, 2011) but also enhances dopamine release (e.g., Hart et al., 2015; Linnet et al., 2012; Zack et al., 2014). These effects suggest that uncertainty has incentive properties. If the view presented here is correct, the extra dopamine release (as well as its extra behavioral correlates) typically observed during or after exposure to reward uncertainty, compared to individuals exposed to reward certainty, should result from HPA activation. Dopaminergic neurons have receptors to glucocorticoids (e.g., Gustafsson et al., 1987; McEwen et al., 1986), and show increased activity in response to situations that typically activate the HPA axis, both in the ventral striatum and the prefrontal cortex (e.g., Dunn and File, 1983; Rougé-Pont et al., 1998; Piazza et al., 1996; Thierry et al., 1976). Accordingly, the dopaminergic effects observed in situations of manageable challenges may specifically depend on glucocorticoids (Barrot et al., 2000; Cabib and Puglisi-Allegra, 2012; Marinelli and Piazza, 2002).

Glucocorticoids and dopamine are also released in the absence of a challenge, but, in this case, they could operate independently. For example, corticosterone is enhanced in sign-tracker rats autoshaped under reward certainty, in comparison with rats for which lever insertion and food delivery are uncorrelated (Tomie et al., 2002, 2004). Sign-tracking behavior therefore recruits corticosterone, in addition to the classic dopaminergic response. However, these studies do not tell us whether the implication of the HPA axis under reward certainty relates to incentive salience. To test this, corticosterone levels have to be compared between sign- and goal-trackers, which respectively attribute and do not attribute incentive salience to cues. The literature on this

question remains limited. But some findings, obtained after reward certainty training, show that sign-tracker rats have concentrations in plasma corticosterone similar to goal-tracker rats (Lopez et al., 2021)—suggesting that glucocorticoids are unimportant for incentive salience attribution to cues. In another study, Turfe et al. (2024) found that administration of corticosterone increased sign-tracking in rats, sometimes in a vendor-dependent manner. However, corticosterone did not change the expression of the conditioned response, when nose poking gave the rats the opportunity to cause insertion of the lever CS. They concluded that corticosterone influences dopamine transmission in the nucleus accumbens and promotes the acquisition rather than the expression of sign-tracking. Based on the view presented here, I would suggest that corticosterone does not alter incentive salience attribution and does not alter learning directly, but may create a perception of challenge that increases and varies the interactions with the lever—as observed in sign-tracker rats under reward uncertainty (Anselme et al., 2013; Robinson et al., 2014). More effective learning would simply result from these behavioral effects—as reported earlier, creative solutions are more likely to be learned using this strategy (e.g., Benson-Amram and Holekamp, 2012; Griffin et al., 2014; van Horik and Madden, 2016). Other findings also support the limited impact of corticosterone on the cue- and reward-triggered behavior: The antagonism of glucocorticoid receptors by specific drugs has little effects on sign-tracking under reward certainty (Rice et al., 2018) and reward approach (Saal et al., 2003).

5.3.1. The importance of manageable challenges

Aside unchallenging situations are situations that offer a challenge. Here, glucocorticoids come to influence dopamine release, but the resulting dopaminergic effects depend on whether the challenge is manageable or not. The salutary effects of manageable challenges should not be confounded with the deleterious stressful effects of prolonged uncontrollability (Sapolsky, 2015). In this latter case, the situation ceases to be a source of stimulation, reducing noradrenaline levels in the prefrontal cortex and inhibiting dopamine levels in the nucleus accumbens—though, not in the prefrontal cortex (Cabib and Puglisi-Allegra, 2012). Severe, chronic stress has detrimental effects on motivation and exploration; it tends to reduce behaviors such as reward seeking, locomotion, and parental commitment (Dieterich et al., 2021; Lemos et al., 2012; Lendvai and Chastel, 2010; Spring et al., 2021). Injecting HPA hormones such as CRF at a high dosage (Lemos et al., 2012) or the optogenetic stimulation in CRF-containing brain areas such as the bed nucleus of stria terminalis (Baumgartner et al., 2021), reduces dopamine release and a panel of motivated behaviors in a way that reflects a severe stress response. The individuals receiving such treatments behave as if they had to face unmanageable challenges. It is interesting to note that people with chronic depression also have higher cortisol levels, especially in the afternoon (Burke et al., 2005), and that higher morning cortisol levels are predictive of major depression development later in adolescence and young adulthood (Zajkowska et al., 2022). These HPA-related effects may explain the difficulties that people with chronic depression have in managing their life, as well as their general feeling of hopelessness (e.g., Alloy and Clements, 1998): The challenges they encounter seem insurmountable. In agreement, they also show blunted reward anticipation and willingness to exert physical effort for potentially larger rewards (Treadway et al., 2012).

In contrast, moderate doses of HPA hormones or the optogenetic stimulation of CRF-expressing neurons in the central amygdala and the nucleus accumbens increases dopamine release and positively stimulates motivated behaviors (Baumgartner et al., 2021; Cabib and Puglisi-Allegra, 2012; Lemos et al., 2012; Oswald et al., 2005; Pecina et al., 2006; Piazza et al., 1996; Sinha and Jastreboff, 2013). Inducing HPA activation artificially may promote the perception of challenges that do not exist.

It is worth noting that the model presented in Fig. 3 does not make specific predictions about the populations of dopamine neurons

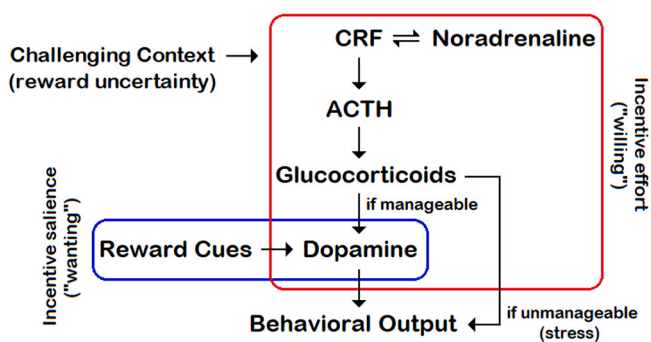


Fig. 3. Incentive effort or “willing” (red frame) complements incentive salience or “wanting” (blue frame). Both mechanisms involve dopamine as being the major modulator of incentivized behavior. But incentive salience insists on the role of cue-reward consistency and reward amount in releasing dopamine, while incentive effort insists on the challenging role of reward uncertainty in releasing dopamine through HPA activation. At one extreme (unchallenging situations), the HPA axis is under-activated and cues induce approach behavior through dopamine release. At the other extreme (unmanageable challenges), the HPA axis is over-activated and dopamine is no longer released, causing severe stress symptoms such as behavioral inhibition and stereotypies. The interaction between these two systems generates incentive effort, with emergent properties (irreducible to those of the two systems) capable of providing an adaptive response to manageable challenges.

stimulated by glucocorticoids. In the nucleus accumbens, novel events and short-lasting environmental challenges cause tonic dopamine activation of D2 receptors in the shell but not in the core region (Cabib and Puglisi-Allegra, 2012). Also, the dorsomedial striatum (caudate) seems particularly sensitive to reward uncertainty and effort in humans (e.g., Bjork and Hommer, 2007; Suzuki et al., 2021), and excitotoxic lesions of this brain nucleus in rats abolish extra responding to a lever CS under reward uncertainty in Pavlovian autoshaping (Torres et al., 2016). Interestingly, in humans, activation of the dorsal striatum (caudate-putamen) is proportional to the magnitude of the expected reward, but inversely proportional to its probability (Miller et al., 2014).

Only a few studies have examined both glucocorticoid and dopamine release in a context of active foraging. In this respect, interesting results were reported by Duclos et al. (2009), (2013). In rats, food restriction stimulates running behavior in an activity wheel. These authors found that healthy rats fed with saccharin (a non-nutritive substance), as well as adrenalectomized rats injected with corticosterone, showed a noticeable increase in wheel running—compared to their control counterparts. In other words, the invigoration of wheel running occurred in food-restricted rats improperly fed or supplied with corticosterone following removal of their adrenal glands. Duclos et al. (2013) also found that wheel running in food-restricted, but not in food non-restricted, rats was positively correlated with a higher number of c-Fos cells in the nucleus accumbens, indicating a stronger activity of dopamine receptors in this brain area. The incentive effort hypothesis predicts that those effects reflect glucocorticoid-induced dopamine release, because food restriction is a typical consequence of challenging uncertainty that stimulates effortful foraging in nature—here possibly observed in the form of wheel running in captive individuals. Of note, restricting the daily access to a running wheel instead of the access to food also seems to recruit corticosterone and dopamine (Ebada et al., 2016). These effects might result from the same process, assuming that, in these conditions, rats perceive a limitation in their ability to search for other profitable opportunities despite the food available—a situation that might correspond to thwarted contrafreeloading. The lack of opportunity to be exposed to biologically relevant challenges is possibly a major reason why captive animals in zoos develop pathologies such as behavioral stereotypies or gastric ulcerations (e.g., Clark, 2012; Meehan and Mench, 2007).

It is also interesting to compare dopaminergic innervation in the brain of passerine birds (sparrows, tits, blackbirds, etc.), which are very active in searching for food and are constantly moving from one place to another during the day, with that of more placid bird species such as pigeons and chickens. In a neuroanatomical study, von Eugen et al. (2020) found that zebra finches (*Taeniopygia guttata*) and carrion crows (*Corvus corone*)—two passerine species—have widespread dopaminergic innervation of their brain, with three (perhaps four) separate areas of a distinct high fiber density that span across the entire caudolateral nidopallium—the functional equivalent to prefrontal cortex in birds. In contrast, they found a poorer dopaminergic innervation in the brain of pigeons (*Columba livia*) and chickens (*Gallus gallus*), limited to a single structure within the caudolateral nidopallium. A strong dopaminergic innervation in this brain nucleus is predicted to correlate with intelligence (Güntürkün et al., 2024), but might also contribute to motivate the higher activity level typically observed in small passerines relative to other bird species. In this respect, it is worth noting that the propensity to engage in new foraging tasks and the capacity to find innovative solutions to various problems seem to depend on motivational rather than cognitive factors (e.g., Benson-Amram and Holekamp, 2012; Griffin et al., 2014; van Horik and Madden, 2016).

The study by von Eugen et al. (2020) did not examine corticosterone levels, but the incentive effort hypothesis predicts that they should be higher in passerines than in pigeons and chickens during their activity period. In agreement, corticosterone-implanted mountain chickadees (*Poecile gambeli*) cached and consumed more food than placebo-implanted individuals (Pravosudov, 2003). This suggests that,

in addition to showing more efficient spatial memory for cache recovery, corticosterone-implanted birds had a higher motivation to search and cache food items. Corticosterone might therefore play a significant role in the adaptation to unpredictable environments (Bonier et al., 2009; Pravosudov, 2003). In a similar vein, during chick-rearing in female tree swallows (*Tachycineta bicolor*), a positive relation between baseline corticosterone and resting metabolic rate was found and they were associated with a higher reproductive investment (Jimeno et al., 2020). In free-living house sparrows (*Passer domesticus*), only individuals with low pre-breeding but high breeding baseline corticosterone concentrations raised more fledglings (Ouyang et al., 2011; see also Bonier et al., 2007). Although corticosterone levels do not appear to change reproductive strategies per se, they boost parental effort and hence the ability to meet the challenge of raising more fledglings (Ouyang et al., 2011, 2013).

5.3.2. A testable hypothesis

The major prediction of the incentive effort hypothesis is that only manageable uncertainty-induced effort involves both glucocorticoids and dopamine. In this case, effort is not a cost and produces a will-like effect aimed to meet the challenge through curiosity and exploration. Effort may even be preferred to its absence, like in contrafreeloading situations—without pretraining with the effortful option to avoid effort justification as a plausible explanation. In contrast, dopamine without glucocorticoids produces “wanting” and glucocorticoids without dopamine induces stress—two situations in which effort is costly and not preferred. Given the high temporal resolution of optogenetic stimulation, multiple experiments could reveal the involvement of CRF and dopamine in challenging situations. For example, inhibiting CRF and dopamine neurons during lever insertion under reward uncertainty is predicted to reduce Pavlovian responses more than inhibiting CRF or dopamine neurons separately. Also, activating CRF neurons during lever insertion under reward certainty should increase the number of Pavlovian responses compared to sham rats under reward certainty.

This interpretation of the responses to reward uncertainty also invites us to think about behavior outside of a Skinner box. Experimental conditions in which animals show a release of glucocorticoids and dopamine might be indicative of exploratory search—even if the observed behavior looks different due to schedule-induced constraints. We already mentioned wheel-running behavior in food-restricted rats as a possible occurrence of food seeking (c.f., Duclos et al., 2009, 2013). But many other situations pose similar questioning, which could be tested separately and possibly reinterpreted. For example, I predict that animals tested under reward uncertainty in autoshaping should release more glucocorticoids (in addition to more dopamine), compared to rats tested under reward certainty. This means that their enhanced responses to a lever CS should be indicative of reward search instead of cue approach in a more naturalistic environment. So, uncertain rats that do not show enhanced responding in autoshaping are predicted to produce not enough glucocorticoids or dopamine or both. It is worth noting that Fuentes-Verdugo et al. (2020) found similar response rates during autoshaping acquisition in two strains of inbred Roman rats (whether exposed to reward uncertainty or certainty), one in which rats produce high glucocorticoid levels and low dopamine levels, and the other in which rats have the opposite neurobiological profile. However, in a next step, the uncertain rats were more resistant to extinction than their certain counterpart. Resistance to extinction was even more pronounced in uncertain dopaminergic rats than in uncertain rats producing more glucocorticoids. This result suggests that the extinction phase was more challenging after uncertainty training—especially for the hyperdopaminergic rats—than the acquisition phase.

Another example is the extinction burst, where autoshaped rats under reward certainty—but not reward uncertainty—often show a sudden increase in their response rates during the first extinction session. Although sometimes explained in terms of frustration, because associated with a higher release of glucocorticoids (Thomas and Papini,

2001), the extinction burst might instead be caused by a transient perception of challenge, due to the sudden ambiguity of the CS (Anselme, 2022). Pet owners sometimes amuse themselves by repeatedly showing an object to their pet, then quickly hiding the object as if it had disappeared. The animal's first reaction is surprise, and then it starts looking for the object. Funny videos on the Internet show that this search behavior can be observed with dogs, cats, monkeys, but also parrots and other species. In this context, search behavior could correspond to the extinction burst, revealing what the activity burst early in extinction may mean in a natural setting. The following experiment could test this idea. In Pavlovian acquisition, rats are repeatedly exposed to three levers—one is retractable and its presentation is always followed by food delivery (reward certainty), while the other two (control) levers are never retracted. Rats should quickly focus their attention on the retractable lever over the training sessions. In extinction, the same three levers are available but the presentations of the same retractable lever are no longer followed by food delivery. If the extinction burst typically observed during the first extinction session relates to exploration, we should observe more frequent responses to the control levers during this session than late in the acquisition phase. Glucocorticoid and dopamine levels should also be increased during this session than late in the acquisition phase.

6. What about intention as a component of will?

Desire, pleasure, and will are typically viewed as conscious mental states, and it is now well established that desire and pleasure have an unconscious counterpart (e.g., Berridge, 2007)—referred to as “wanting” (cue-triggered approach induced by dopamine) and “liking” (hedonic reactions—e.g., facial expressions during consumption—induced by other neurotransmitters), respectively. Until now, fewer scientific studies have been conducted about will, but the suggestion that will also has unconscious roots is not new and empirical supports for it have accumulated. Custers and Aarts (2010) wrote: “the scientific study of goal pursuit has discovered that these processes can also operate without conscious awareness, and hence, human behavior may originate in a kind of unconscious will” (p. 47). For example, Bargh et al. (2001) asked participants to play against a presumed opponent, in a task in which they had to share a limited resource pool (i.e., fish in a lake). Participants could use a competitive strategy (maximize self-profit), a cooperative strategy (maximize common good), or a mixture of both. Half of the participants were primed with words related to cooperation (e.g., honest, support, share), while the other half was primed with neutral words relative to cooperation (e.g., salad, wet, zebra). In these two groups, half of the individuals were explicitly asked to collaborate in the task and the other half received no specific request. The authors found that participants primed for cooperation in the unconscious-goal condition showed the same increase in cooperation than participants primed for cooperation in the conscious-goal condition, suggesting that cooperation as a goal can be achieved independently of consciousness. They concluded that goals can be activated unconsciously.

The scientific literature on will posits that intention (whether conscious or not) underpins goal pursuit. But is will reducible to intention? And is intention equivalent to incentive effort or “willing”? I would like to explain why the answer to these two questions is *No*. First, intention is a cognitive state rather than a motivation. In the words of Berridge (2012): “knowledge by itself, no matter what kind, is never motivation. Something else is required to translate remembered knowledge into motivation that can actually generate and control behavior” (p. 1124). Thus, intention is, by principle, not close to action. I may intend to cut the hedge in my garden or to clean the garage of the house but not much excitement for those activities. Procrastination is a typical example of intention without motivation, the person constantly postponing the activity to the next day. Intention actually relates to the planification of action but having a plan for a future action does not

mean that the plan will be followed and the action carried out. In other words, intention does not contain the self-determination typically associated with will and cannot therefore be the same thing as will. Second, contrary to self-determination such as defined earlier in this paper (see also Table 1), intention is insensitive to reward uncertainty. The intention to do an activity is independent of whether its outcome is guaranteed or not (e.g., trying to repair one's lawnmower), or even whether the action is desired or just mandatory (e.g., accepting to do boring tasks to keep one's job). Intention can be formed in a challenging context, but is not specifically a response to a challenge. In contrast, voluntary action is a response to a challenge because this is what distinguishes it from cue-triggered behavior. For example, passing a difficult exam is a challenge that requires voluntary investment, while eating the ice cream in the freezer is a product of incentive salience attribution to perceived or recalled cues. In short, self-investment requires a challenge but intention does not; incentive effort is not equivalent to intention.

7. Summary and conclusion

In this paper, I have presented incentive salience (“wanting”) as the directional component of incentive motivation, because it makes reward cues attractive and approached (cf. sign-tracking behavior). Incentive salience relates to Pavlovian conditioning and might underpin desire as a conscious mental state. It was shown that this process, as well as instrumental expectations, do not account for the energetic component of motivation in a context of reward uncertainty, which creates a challenge for organisms. It has been hypothesized that this energetic component in response to a challenge has to do with the core process of will, another motivational aspect poorly discussed beyond cognitive issues such as intention and goal pursuit. Incentive effort (“willing”) would capture this core process, consisting of a self-determination to achieve a “wanted” action. Shortly, incentive effort is the missing piece between the absence of behavioral control (incentive salience) and behavioral control (instrumental expectation); it reflects cue-based attempt to get control when this opportunity is uncertain.

The originality of this view consists of linking the core psychological process of will to the so-called stress system (HPA axis), which would be more appropriately defined here as a functional adaptation to environmental challenges instead of physiological reactions to stressors. Stress would only result from prolonged exposure to unmanageable challenges, causing a decrease in wellbeing. This interpretation has the advantage of proposing a reason why the HPA axis was shaped by evolution, instead of having to distinguish good and bad stress (acute, moderate vs. chronic, intense HPA activation) and to struggle with the unlikely adaptiveness of bad stress. Assuming that this interpretation is correct, there must be considerable constraints on the existence of free will, a topic that has been debated by philosophers and scientists for centuries. It is not the place to discuss this question in a conclusion. But the present view leads us to think that self-determination and desired actions do not primarily originate in consciousness; they are not causeless causes. They are constrained by our psychobiological organization and preexist, in the form of unconscious processes, before emerging in our conscious experience and giving us the illusion that our introspective Self is in charge of our decisions and actions. As counter-intuitive as it is to say that we may want and like unconsciously, it seems that we can only will what our brain machinery allows us to will. As Schultz (2015) noted: “It would be advantageous to seek [...] hidden rewards actively rather than waiting for them to appear out of the blue. [...] Without the true or false belief of free will, we may have only limited initiative to find hidden rewards” (p. 933).

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Data availability

No data was used for the research described in the article.

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