

REVIEW

Is Our Self Nothing but Reward?

Georg Northoff and Dave J. Hayes

Neuroscience has increasingly explored the neural mechanisms underlying our sense of self. Recent studies have demonstrated the recruitment of regions like the ventral tegmental area, ventromedial prefrontal cortex, and the ventral striatum to self-specific stimuli—regions typically associated with reward-related processing. This raises the question of whether there is a relationship between self and reward and, if so, how these different fields can be linked. Three relationship models that aim to explore the relationship between self and reward are discussed here: integration, segregation, and parallel processing. Their pros and cons are reviewed in light of the most recent findings. The conclusion is that both the fields of self and reward may benefit from increased interaction. This interaction may help to fill in some of the missing pieces regarding reward-related processing, as well as illuminate how brain function can bring forward the philosophical concept and psychological reality of self.

Key Words: Animal, human, models, psychiatric disorders, reward, self, translational

Though the self is originally a philosophical concept, it has become the subject of intense neuroscientific investigation, especially in neuroimaging (1–3). This research has revealed that several brain regions—collectively referred to as cortical midline structures—like the ventromedial prefrontal cortex (VMPFC), dorsomedial prefrontal cortex (DMPFC), anterior cingulate cortex, and the posterior cingulate cortex, are recruited during exposure to self-specific stimuli when compared with nonself-specific ones. (Self-specific stimuli are considered to be those that an organism identifies as highly personally relevant.) However, there has been some doubt about the strict association of the cortical midline structures with self-specific stimuli because some familiar and unfamiliar nonself-specific stimuli also induce activity changes in these regions (4,5).

Recent studies on self and reward have demonstrated that self-specific stimuli induce neural activity changes in regions recruited during reward, e.g., VMPFC, ventral striatum (VS), and ventral tegmental area (VTA) (6–9). The apparent overlap in neural activations between self-specificity and reward raises several questions regarding their relationship. For instance, is self-specificity nothing but reward? In other words, does self-specificity really amount to those things that have high degrees of value for us? Do we need to consider that the existence of the self is an illusion as argued by some philosophers (10)?

Despite an increased understanding of the variety of functions subsumed under the concept of reward (11,12), several issues remain open in this field. For instance, Montague (13) has pointed out the relevance of linking incoming exteroceptive stimuli to the body's interoceptive stimuli by assigning value, and thus reward, to the former. This may be crucial because the exteroceptive stimulus' rewarding features may also depend on the organism's actual states and hence its interoceptive stimuli. Self-specificity may be constituted by linking interoceptive and exteroceptive stimuli (6), which may allow a certain continuity over longer time intervals (i.e., self-continuity; see Ersner-Hershfield *et al.* [7]). Hence, some of the

open questions in the field of reward may interface with issues and problems raised in the field of self.

The aim of this article is to explore the interface between reward and self by discussing different models of their potential relationship. Based on the actual data, we propose three different models of the relationship between self and reward to structure the abundance of current empirical findings in both domains: overlap between self and reward (i.e., the integration model), nonoverlap between both (i.e., the segregation model), and self as parallel processing at some level (e.g., higher or lower order processes) along a reward continuum (i.e., the parallel processing model) (Figure 1). Evidence across studies supporting and refuting each model will be offered and discussed. Along with evidence in humans, some nonhuman animal studies that have implicated the involvement of similar brain regions in reward-related, and potentially self-specific, processing will also be considered. It is also important to note that although the translational evidence discussed may support one model or another, the original investigators of each study under consideration may not agree with such an approach; as such, it is acknowledged that other possible interpretations may exist. Finally, the potential impact of considering the relationship between self and reward on psychiatric disorders, such as addiction and depression, is indicated (see Table 1 for summary and Supplement 1 for a more in-depth discussion).

Reward-Self Relationship Models

Before discussing the reward-self relationship models, it is important to note that the terms reward and self are used here in a very basic sense (compared with the various uses within their respective fields; for examples in the field of reward, see [14–17]). One core component of reward is value assignment, meaning that an external stimulus is assigned specific relevance or importance for the organism (18,19). Similarly, although there are numerous aspects of the self (e.g., self-recognition, self-consciousness, self-awareness), the use in the present work refers largely to the fact that some stimuli are self-specific. This basic or core aspect of self can be considered the primal characterization of the organism in relation to the environment, and thus, this concept may be shared among humans and other animals (20).

First Model: Integration of Self and Reward

The integration model of self and reward claims that our self is almost entirely reward; that self-specific stimuli are really those that have a high level of value assignment for us. Self-specificity may thus be constituted and distinguished from nonself-specificity by the value of the stimuli. This may hold not only for external stimuli from the environment but also for internal (i.e., interoceptive/bodily and cognitive/mental) stimuli. These too must be assigned a

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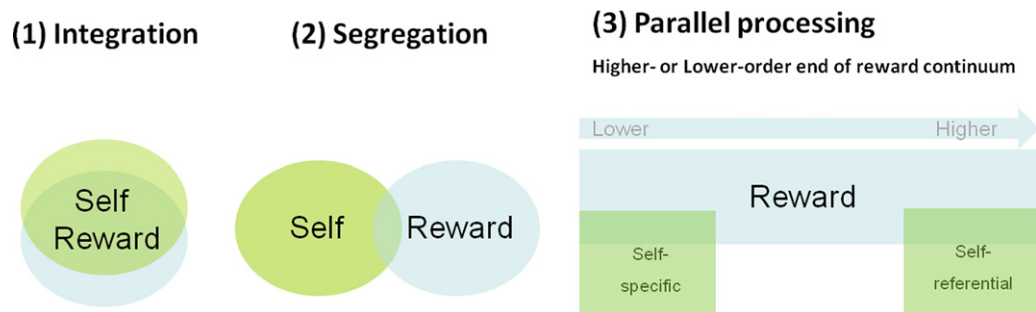


Figure 1. Relationship models of self and reward. The integration model (1) describes a relationship where self-specific and reward-related processing are nearly identical, whereas the segregation model (2) describes a relationship where they are nearly unrelated. The parallel processing model (3) describes a relationship whereby the various aspects of self (e.g., self-specificity) are processed in parallel (i.e., temporally and spatially in an interconnected way) with lower order reward-related processing—suggesting that this relationship combines elements of both the integration and segregation models.

value to be self-specific and distinguished from nonself-specific ones. Hence, value assignment to stimuli is not only at the core of reward but may also be crucial in constituting self-specificity and its distinction from nonself-specificity.

Support for the integration model comes from human imaging studies by Phan *et al.* (8) and de Greck *et al.* (9). Phan *et al.* (8) showed that during the viewing of emotional pictures, neural activity changes in the VS and the VMPFC are linearly dependent on the degree of self-specificity assigned to the pictures by the subjects. While that study did not test for activity changes related to reward, de Greck *et al.* (9) demonstrated that self-specificity induced activity changes in these regions (i.e., VTA, VS, VMPFC), thus demonstrating an overlap of areas recruited during self and reward processing. Two studies by Enzi *et al.* (6) and Ersner-Hershfield *et al.* (7) observed the involvement of other regions, including the pregenual anterior cingulate cortex (PACC), ventrolateral prefrontal cortex, and the caudate nuclei, during self- and reward-related tasks. Enzi *et al.* (6), in particular, did this in an interesting way by investigating changes in blood oxygenation level-dependent (BOLD) signaling during closely interleaved trials involving reward-related (i.e., a gambling task), self-specific (i.e., a personal relevance evaluation task), and control tasks (i.e., determining the orientation of a visual stimulus). Finally, a recent study in a group of young adults (aged 15–24) found that the

social aspect of being liked by one's peers activated reward-related and self-specific (i.e., midline) regions. In particular, activations were noted in VS, midbrain (in an area corresponding to the VTA), VMPFC, posterior cingulate cortex (including retrosplenial cortex), amygdala, and insula/opercular cortex, while subjects showed greater activation in the VMPFC and amygdala in response to being liked by those whom they regarded highly (21).

Given that nonhuman animal research has largely not explored the concept of self (beyond some work on self-recognition and awareness, e.g., see [22–24]), it is challenging to directly compare reward-related processing and behavior—which has been investigated extensively—with that of the self. Although tested indirectly, it may be useful to interpret some animal studies investigating reward-related processing as having self-specific components. To help illustrate this point, consider the following analogy: the grand piano has high personal relevance for the pianist in the same way that a running wheel may have high personal relevance for a rodent; this can be determined, for instance, by assessing the time spent (behavioral) and physiological responses during the free pursuit of such things. Though one could argue that the pianist can be directly asked about this relevance, while the rodent cannot, evidence indicates that self-specific and reward-related associations need not require aware-

Table 1. Self and Reward in Psychiatric Disorders

Psychiatric Disorder	Role of Self and Reward	References
Addiction	Self-specific stimuli produced BOLD signals in reward circuitry (e.g., VTA, VMPFC, and VS) in healthy subjects; alcoholics and pathological gamblers displayed normal reward circuitry activity during a reward-related task but no changes during a self-specific task (i.e., the judgment of stimuli as self- or nonself-specific).	(9,32,33)
Depression	Human and animal data of depressive-like behaviors show increased resting state activity in midline regions (e.g., PACC, VMPFC, VS) that are also implicated in self-specificity and reward-related processing. Reduced responding of reward-related and self-specific areas (e.g., VS, DMPFC) to positive stimuli in depressed subjects has also been noted and is in line with the increase in self-focus, or ruminations, seen in this disorder. It appears as though GABAergic and glutamatergic functioning may play an important role.	(67–72)
Schizophrenia	Patients show inappropriately strong VS activations to neutral stimuli in an aversive learning paradigm. Behaviorally, they also show increased temporal discounting and decreased motivation (or wanting), although their subjective experience of rewards may be intact.	(73–76)
Borderline Personality	Patients show no PFC (e.g., OFC, DLPFC, anterior cingulate) responses during a reward task and reduced (e.g., OFC) or increased (e.g., anterior cingulate) responding during a punishment task over healthy control subjects. Interestingly, a separate study found that these patients show hyperactivity in OFC and anterior cingulate to both self-specific (or autobiographical) and neutral stimuli, suggesting a deficit of selective activation.	(77,78)

BOLD, blood oxygenation level-dependent; DLPFC, dorsolateral prefrontal cortex; DMPFC, dorsomedial prefrontal cortex; GABA, gamma-aminobutyric acid; OFC, orbitofrontal cortex; PACC, pregenual anterior cingulate cortex; PFC, prefrontal cortex; VMPFC, ventromedial prefrontal cortex; VS, ventral striatum; VTA, ventral tegmental area.

ness (as noted below), suggesting that behavioral and physiological measures are invaluable in this regard.

With that in mind, many animal studies have demonstrated that VS neurons fire to, and in anticipation of, reward-related stimuli (25). However, there is also a growing body of literature indicating that representations of reward that may be personally relevant to the organism produce activations independent of reward receipt alone (e.g., organism-specific reward-related memories). For example, one study in rats found that the reactivation of memory traces not only activates feature- and context-specific information but also contains a value-associated component, indicating that activations associated with the memories of personally relevant stimuli are tied directly to reward-related processing (26). In another study, local field potential oscillations in the rat VS were investigated (27). Results indicated distinct oscillations associated with reward-related memories (70–85 Hz) versus those associated with reward receipt and reward-related movement initiation (45–55 Hz). These results are in line with the other human data, noted above, and suggest that memories for individual experiences directly involve reward-related processing.

Does this mean that our self is thus nothing but reward? We have to be careful with this conclusion because the empirical support is not uncontroversial. For instance, many studies have also uncovered evidence that may be taken to support a nonintegrative model—as outlined in the segregation model section below. Conceptually, the integration model leads to a consideration of the concept of self in terms of value-awareness. To this, one could logically argue that value assignment does not require an explicit awareness of value, because the former does not necessarily entail awareness or consciousness and also occurs at an implicit (i.e., unconscious) level (28,29). In contrast, the concept of the self, as described throughout the literature, seems to be linked to consciousness (however, as demonstrated below, the self may also be developed and maintained implicitly/without awareness).

Together, the results from human and nonhuman animal studies show some support for the integration model, given the possibility that at least some aspects of self-specific and reward-related processing occur through integrated mechanisms. Nonetheless, there is also evidence to the contrary. This issue is further amplified by considerations of potential differences between the self and reward on the conceptual level. Hence, we turn to the possibility that the self and reward are largely separate entities by outlining some support for the segregation model.

Second Model: Segregation Between Self and Reward

Contrary to the integration model, the segregation model of self and reward claims that our self-specific processing is almost entirely independent of reward-related processing. This suggests that self-specific stimuli are really processed independently from the general valuation processes associated with all self- and nonself-specific stimuli. Value assignment and self-specificity assignment may then be regarded as different processes that are regionally and temporally segregated.

Evidence from both human imaging and nonhuman animal studies appears to support key aspects of the segregation model. For instance, the study by de Greck *et al.* (9), noted above, points out some differences in the duration of the BOLD response associated with self-specific and reward-related processing in humans. Based on raw data analysis (rather than model-based analysis), the authors observed sustained BOLD signals during the processing of self-specific stimuli in the above-mentioned reward circuitry (e.g., VTA, VMPFC, and VS), while reward-related stimuli induced shorter and more phasic signals in the same regions. This finding, however,

must be considered preliminary because of the sluggishness of the BOLD response, which currently make it difficult to associate neural timings with precision (for an in-depth discussion on related methodological issues, the reader is referred to [30,31]).

Nonetheless, this group went on to further substantiate the possible dissociation between self-specific and reward-related processing in psychiatric patients (Table 1; refer to Supplement 1 for a more in-depth discussion). They observed that while both detoxified alcoholic patients and pathological gamblers displayed normal neural activity changes in VMPFC, VTA, and VS during a reward-related task, they nevertheless showed no activity changes in these same regions during a self-specific task (i.e., the judgment of stimuli as self- or nonself-specific) (32,33). The assumption of a regional difference between self-specific and reward-related processing is further supported by Enzi *et al.* (6). In this study, the authors found that regions such as the insula, premotor cortex, and the supragenual anterior cingulate cortex were exclusively associated with the processing of self-specific stimuli as distinguished from reward. Taken together, these findings in humans do indicate a possible dissociation between self and reward either within the same regions (e.g., reward-related circuitry) or across different regions (e.g., the insula or premotor cortex).

There may also be some evidence to support the segregation model in studies of nonhuman animals. For instance, it could be argued that the work by Berridge *et al.* (15) on differentiating between various components of reward, such as liking, wanting, and learning are also investigating brain-related activity for stimuli that are both self-specific and reward-related. This group has presented strong evidence of a dissociation between wanting (i.e., incentive salience or the motivation to approach reward-related stimuli, which may involve self-specific processing) and liking (which reflects the hedonic impact of rewarding stimuli) circuitry. They have shown a rostrocaudal spatial separation between the circuitry of wanting and liking in both the VS (34,35) and the ventral pallidum (36). Additionally, the ventral tegmental area-substantia nigra complex (37) and amygdala (38) have also been implicated in this regard. On the human side, Knutson *et al.* (39) developed the monetary incentive delay task, which includes an anticipation period as part of a reward task; interestingly, the anticipation period does indeed induce strong activity in the typical reward regions (e.g., VTA, VS, VMPFC) even before the reward is actually received (40). Whether such an anticipatory period modulates or even simulates activity related to what is described by Berridge *et al.* (15) as wanting in animals, however, remains open.

Congruent with the data from alcoholic patients and pathological gamblers above, some stimuli (i.e., drug-associated cues) take on high incentive salience (wanting) roles but have low reward (liking) values in animals in addicted-like states (what Robinson and Berridge [41] have termed incentive sensitization). These behavioral observations (e.g., via drug self-administration) are supported by the evidence implicating, for instance, dysregulation of the VS in mediating the abnormal wanting, but not the liking, component in animals trained to associate cues with the reception of drugs of abuse (42,43). This incentive sensitization results in what these authors refer to as an irrational wanting for something that is not cognitively wanted (15). Importantly, this dissociation is in line with that seen in alcoholic patients and pathological gamblers showing normal VS function in the reward-related task but abnormal responding during the self-specific task (9,33).

As with the integration model, there are some conceptual considerations and caveats regarding the segregation model. For instance, it is tempting to speculate that there may be no self-specific component to liking (i.e., the hedonic impact of rewards), given that

it does not require conscious awareness (28,44). On the other hand, there may be a self-specific component to wanting, given that this concept reflects the level of importance placed on external stimuli by the organism. Additionally, contrasting the results from healthy versus addicted-like animals and humans suggests that at some level self-specific and reward-related processing are segregated and can become dysregulated (as reflected in addicted-like states). Nonetheless, while there is strong support for the distinction between liking and wanting regarding reward-related processing and the data from these studies may be in line with the presence of self-specific processing, there is currently no direct evidence for (or against) the involvement of a self-specific component. Hence, we consider a third model, which attempts to reconcile the support for each the integration and segregation models.

Third Model: Parallel Processing of the Self Along the Reward Continuum

The parallel processing model aims to account for all the observations noted above by considering that different aspects of self-specific processing may occur in parallel with aspects of reward-related processing. As alluded to above, the full spectrum of reward-related processing involves different neural substrates (including both cortical and subcortical areas), as well as a range of temporal responses (early vs. later phase responses). Intuitively, it could be hypothesized that various aspects of the self are processed in parallel along a continuum of reward-related processing (Figure 1). Next, we will weigh the evidence and conceptual considerations for this model by focusing on (what we have termed here) the lower-order end of the continuum. At this extreme, self-specific processing could be considered the ground upon which the assignment of value to external stimuli becomes possible. This lower order designation may reflect the basic processing that dominates mainly (but perhaps not exclusively) in subcortical regions and earlier in time. Although self-specific processing may take place at other levels of the continuum, we have not considered this here in depth (although the section ends with a brief note on the higher order end).

From an anatomical viewpoint, imaging studies demonstrate the involvement of subcortical regions like the periaqueductal gray, the VS, putamen/caudate, the tectum, and the VTA in self-specificity assignment (6,8,9,45–47). This is particularly seen in studies that rely on passive perception, as opposed to more cognitive involvement in which subjects have to explicitly judge the stimulus' degree of self-specificity. Conversely, reward and value assignment do not only implicate subcortical regions like the VS and the VTA but also various cortical regions including the VMPFC, the lateral prefrontal cortex, and the parietal cortex (48). Hence, the imaging findings do not support the distinction between reward- and self-specific processing strictly along subcortical and cortical borders.

Indeed, the observed overlap between reward- and self-specific processing in the core regions of the reward circuitry (e.g., VS, VTA, VMPFC, and PACC) in humans (6,7,32,33,49) and in animals (26,34,37) further underscores that the concepts of reward and self cannot be strictly delineated through gross neuroanatomy. As another example of this, self-specificity assignment appears to involve specific regions like the insula that have been implicated in the processing of interoceptive stimuli from one's body (6,50–54). This may distinguish it from reward-related processing, which may be more focused on exteroceptive rather than interoceptive stimuli. However, there is evidence of its involvement in reward-related processing, supported by the recruitment of the insula in socially related reward tasks (55,56), as well as by its putative role in subjective drug craving (57). However, the exact relationship between

value and self-specificity assignment in the insula (and other regions), as well as the impact of interoceptive processing, remains unclear (see Supplement 1 for more discussion on the role of interoception).

More support comes from the consideration that the same brain regions may be implicated in different processes at different times. Schultz (14,58) has argued that the activities of dopamine neurons may result in different effects at different time scales. For instance, short phasic increases (reward prediction error), more sustained phasic responses (reward uncertainty), and slower depressions (aversive signaling) are each associated with different aspects of processing. Additionally, slow tonic dopaminergic changes across time intervals of around 20 to 30 minutes appear to broadly affect movements, cognition, and motivation. In a similar fashion, neural activity within regions may mediate different functions (e.g., related to reward and self) at different time scales. In-depth investigation of these time scales and the other transmitters likely involved (e.g., gamma-aminobutyric acid, glutamate, and serotonin) may be best undertaken in nonhuman animals. For this, however, we must first better operationalize aspects of reward- and self-specific processing in animals (see Supplement 1 for more discussion). Although these are methodologically difficult to discern in human imaging paradigms, this would help to explain why there is neural dissociation between self and reward, even within the same regions (9,32,33). If this holds, one could argue that what we call value assignment operating within the millisecond-to-second range may reflect a temporal dissociation from our concept of self-specificity. This, however, remains to be demonstrated (see Supplement 1 for more discussion on the role of temporal coding with regard to the self).

In addition to timing, the broader question of neural coding may also need to be discussed. Reward has also been associated with predictive coding, the notion that the to-be-expected stimulus is anticipated and then matched and compared with the actual incoming stimulus (59). The difference between anticipated and actual stimulus may then reflect what is called the prediction error, which is assumed to determine the degree of neural activity related to that particular stimulus. This has been quite convincingly demonstrated in the case of reward (60,61), while the issue of predictive coding has not been addressed in the context of the self. If reward- and self-specific processing do indeed overlap in terms of regions and neural activity, one would expect the neural activity related to the self to also be determined by the prediction error signaling the degree of mismatch in self-specificity between the anticipated and actual stimulus. This, however, would mean that neural activity in, for instance, cortical midline structures during the perception of self-specific stimuli may rather reflect a difference-based signal, e.g., a difference in anticipated and actual self-specificity, rather than self-specificity per se.

What do these empirical findings entail for the concept of the self as characterized by self-specific processing? The concept of self-specific processing sketched here must be distinguished from the one of self-referential processing that describes the organism's reference to the results of its own stimulus processing (2). The concept of self-referential processing shifts the focus from the more basic and lower order end internal-external organism-environment relationship to a purely internal and therefore higher order end organism-organism relationship (Figures 1 and 2). Hence, the concept of self-referential processing pertains functionally to the meta-representation of what is constituted on the level of self-specific processing. Self-referential processing may then be considered the higher order end, whereby self-specific processing occurs at the

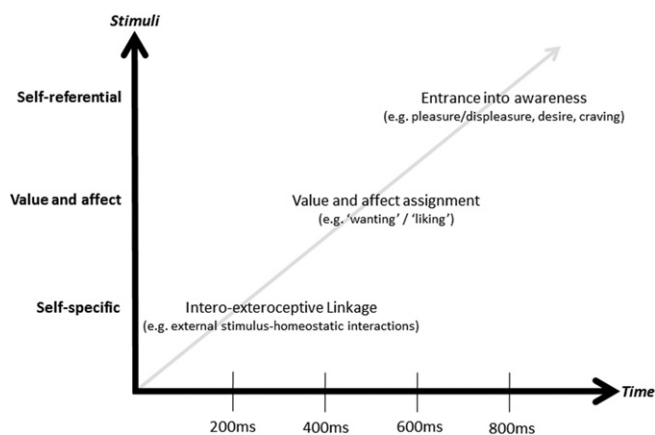


Figure 2. Different functional processes and their hypothesized neural timing. Hypothesized continuous relationship between reward- and self-related processing over time. Note that the examples and related time course are hypothesized and are for illustrative purposes only.

lower order end with both being potentially mediated by value assignment.

Finally, one should also be aware that the concept of reward is currently very different from what it was just a decade ago. While, for many years, the concept of reward was often intimately linked to pleasure (62), recent experiments have described a heterogeneous array of related functions involving pleasure/hedonia/liking, wanting/incentive salience, seeking, instrumental learning, conditioning, prediction, and behavioral activation (12,58,63,64). While reward as pleasure is too general in some way, it may also be too specific by restricting reward to motivational features of positive reinforcers (11). Another concept often closely associated with reward is salience, which refers to the ability of stimuli to induce reallocation of cognitive resources beyond its mere value (see, for instance [65,66]). Defined in terms of resource allocation, saliency may provide a conceptual bridge from reward to the self: stimuli related to the self are highly relevant and important and therefore may recruit and allocate more sensory, affective, and cognitive resources compared with nonself-related ones. However, this remains purely hypothetical at this point and awaits empiric testing. Finally, reward may even be further complicated by considering aspects such as the linkage of interoceptive and exteroceptive stimuli and temporal extension, as may be necessary when considering reward directly with the self. Overall, this discussion suggests that it may not only be the field of self that benefits from turning toward the field of reward but also vice versa.

Conclusions

The discussion of different possible models revealed that self and reward can neither be considered identical (i.e., integration model) nor clearly separate identities (i.e., segregation model). Instead, their relationship seems to be rather complex with multiple interactions across a continuum that may be evident neurally, psychologically, and conceptually. Unfortunately, these results remain tentative, given that the focus on comparisons of self- and nonself-specific stimuli has generated controversy and unclear conclusions. Nonetheless, this makes the future investigation of the interaction between self and reward an exciting field where both may benefit from one another.

By intertwining the fields of self and reward and orienting toward what the empirical data tell us, a far clearer understanding of each concept may emerge. As is already starting to occur in the field

of reward, this may ultimately lead to the determination of the exact processes and psychological functions associated with the concepts of self and reward (for example, involving interoceptive-exteroceptive linkage). This increased interaction and reciprocation between the fields across various levels will undoubtedly lead to exciting new hypotheses and discoveries that will foster the development and refinement of these concepts.

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