

Université de Montréal

Distinction entre besoin et désir
Avec la perspective des neurosciences

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Programme de Ph. D. en Sciences humaines appliquées (S.H.A.)

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Cette thèse intitulée

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RÉSUMÉ EN FRANÇAIS

Le besoin et le désir sont parfois dissociés (discordance), parfois associés (concordance). En effet, le besoin est lié à la privation et, parmi d'autres régions du cerveau, l'hypothalamus et l'insula jouent un rôle central dans l'émanation et la représentation des états de besoin internes de l'organisme, et le niveau de sérotonine semble indiquer les états de privation ou de satiété. Le désir quant à lui est lié à la prédiction de récompense. Cette dernière contrôle davantage le comportement, car elle active les régions centrales de la dopamine : l'aire tegmentale ventrale (VTA) et le nucleus accumbens (NAcc). Cela dit, l'interaction et la différence entre besoin et désir en termes de fonctionnement cérébral ne sont pas si définies, et on ne sait pas vraiment pourquoi parfois il y a concordance et parfois discordance.

Ainsi, la première étude de cette thèse consistait à examiner le patron d'activation cérébrale lié à la perception des stimuli physiologiques et sociaux dont on a besoin, et leurs liens avec la sérotonine. La deuxième étude s'est attelée à comparer les patrons d'activation cérébrale liés à la perception des stimuli liés au besoin, en l'absence de désir ; et celle des stimuli liés au désir en l'absence de besoin. Pour répondre aux deux questions soulevées par ces deux premières études, nous avons utilisé des méta-analyses d'imageries cérébrales fonctionnelles. Nous avons trouvé que les besoins physiologiques et sociaux ont un patron d'activation commun au niveau de l'insula mi-postérieure, de la portion pré-lobique du cortex cingulaire antérieur, et du noyau caudé. De plus, ce patron d'activation commun possède une forte corrélation avec le récepteur 5HT4 parmi les récepteurs de la sérotonine. La deuxième étude a montré que le besoin semble davantage impliquer l'insula mi-postérieure, et que le désir implique les régions de la dopamine, notamment le VTA et le NAcc. Ceci suggère que le besoin dirige le choix et octroie la valeur aux stimuli via la prédiction des états internes ; tandis que le désir dirige le choix et octroie la valeur aux stimuli via la prédiction de récompense. Cette étude montre que ces deux types de valeurs sont indépendants, démontrant que le besoin et le désir peuvent arriver séparément (discordance).

Toutefois, ces deux études n'expliquent pas l'effet sous-jacent du besoin, par lequel il amplifie le désir, le plaisir, etc. Le besoin est lié à la tendance qu'ont les êtres vivants à occuper des états préférés afin de réduire l'entropie. Dans la troisième étude, nous avons utilisé des méthodes computationnelles ; et trouvé que la tendance d'occuper les états préférés est influencée par les états de besoin, indépendamment de la prédiction de récompense ; et que l'entropie est largement réduite en présence d'une récompense menant à l'état préféré qu'en son absence. En effet, l'entropie signifie l'incertitude sur quel état occuper et la précision signifie l'inverse de l'entropie. Comme la dopamine signale la précision qu'une séquence d'événement (policy) mène à la récompense on peut comprendre l'amplification du désir par le besoin : le besoin amplifie le désir si, et seulement si, on est en face d'un stimulus qui signale la précision que la séquence d'événement mène à la récompense, et que cette récompense est la même celle qui réduit l'entropie en menant vers l'état préféré. En ce sens, le besoin et le désir sont en concordance lorsque le stimulus qui mène à l'état préféré est également la récompense prédite, c'est-à-dire celle à laquelle mène la policy.

MOTS CLÉS EN FRANÇAIS : motivation, besoin, désir, prédiction de récompense, croyance, neuroscience, consommation, comportement

ENGLISH SUMMARY

Needing and wanting are sometimes dissociated and sometimes associated. Indeed, needing is related to deprivation, and among other brain regions, the hypothalamus and insula play a central role in the emanation and representation of need states, and serotonin levels seem to encode how deprived or satiated one is. Wanting is linked to reward prediction which has more power on behavioral activation than need states. This is due to the fact that reward predicting cues elicit activity within the mesolimbic dopamine circuitry, especially the ventral tegmental area (VTA) and the nucleus accumbens (NAcc). That being said, the interaction and the difference between needing and wanting as of how the brain works is not fully known, and we can't quite explain why sometimes they are associated and some other times dissociated.

Hence, our first study looked at the brain activation pattern that is common for the perception of physiologically and socially needed stimuli, and the relation between such a common activation pattern and serotonin in the brain. The second study set out to compare the brain activation patterns of the perception of needed stimuli, in absence of wanting, and that of wanted stimuli in the absence of needing. Using functional brain imaging meta-analyses to answer those questions, we found that psychologically and socially needed stimuli have common activation patterns that peaked at the mid-posterior insula, the prelimbic anterior cingulate cortex, and the caudate nucleus. This common pattern has a strong correlation with the 5HT₄ serotonin receptor. The second study showed that needing seems to more consistently activate the mid-posterior insula, whereas wanting more consistently activates dopaminergic regions, especially the VTA and NAcc. This suggests that needing directs choice and assigns value to stimuli via interoceptive prediction; while wanting directs choice and assigns value to stimuli based on reward prediction. The fact that we found these two types of values to be independent shows that needing and wanting can occur separately (they can be dissociated).

However, the first two studies do not explain what the underlying effect of needing is and how such an effect amplifies wanting, liking, etc. Indeed, needing is related to the tendency of living creatures to occupy preferred states in order to reduce entropy. In the third study, using computational methods, we found that this tendency to occupy preferred states is influenced by

need states, independently of reward prediction, and that the presence of a reward leading to the preferred state reduces entropy when need states increase; compared to no reward. As entropy means the uncertainty on which state to occupy, and precision is the inverse of entropy, this result means that need can amplify wanting: it suffices to consider that the prediction of reward triggers dopamine which signals the precision (certainty or confidence) that the policy will lead to reward. It is in this sense that need amplifies wanting if, and only if, there is a cue that signals such precision. In other words, needing amplifies wanting if the reward that leads to the preferred state is the same as the one to which the policy specified by the precision leads to. Otherwise there will be discrepancy, and needing and wanting will happen independently.

KEYWORDS: motivation, need, wanting, reward prediction, belief, neuroscience, computational neuroscience, consumption, behavior

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LISTE DES SIGLES ET DES ABRÉVIATIONS ET ACRONYMES

ACC : cortex cingulaire antérieure

BLA : Amygdale basolatérale

CeA : Noyau central de l'amygdale

Nacc : Noyau accumbens

OFC : cortex orbitofrontal

vmPFC : cortex préfrontal ventromédian

VTA : aire tegmentale ventrale

SN : substance noire

DA : dopamine

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SECTION I : INTRODUCTION

CONTEXTE THÉORIQUE

Selon certains, le niveau de (sur) consommation actuelle serait dû, entre autres, au fait que nous consommons ce que nous désirons au-delà de ce dont nous avons besoin (Stearns, 2006). Au-delà de la perspective de la consommation, la comparaison entre besoin et désir demeure un sujet d'étude qui intéresse nombre de scientifiques provenant de divers domaines de recherche qui se demandent : y a-t-il une distinction entre besoin et désir ? Si oui, quelle est-elle ? Dans cette thèse, je tenterai de répondre à cette question en utilisant l'angle des neurosciences.

Discordance (dissociation) entre besoin et désir

Campbell (1998) rapporte qu'il y a deux types de rhétorique servant à justifier l'action d'achat : celle de besoin et de désir. Le besoin est habituellement lié à un état de privation de quelque chose d'important pour la vie ou la survie (Bouton, 2016 ; Baumeister & Leary, 2017) ; et ne pas y répondre peut entraîner des conséquences néfastes physiologiques ou psychologiques qui vont au-delà de la simple frustration (MacGregor 1960 ; Baumeister & Leary, 1995). Maslow (1943) classe les besoins dans ce qui deviendra une hiérarchie qui commence par les besoins physiologiques et aboutit à ceux liés à l'actualisation. Cependant, de nombreuses études montrent la faillibilité de la hiérarchisation des besoins, et suggèrent que ces derniers fonctionnent de manière plus ou moins indépendante sur le plan motivationnel (Goebel & Brown, 1981 ; Hofstede, 1984 ; Ducourant et Perrin-Heredia, 2019 ; Tay et Diener, 2011). Cela semble dû au fait que les besoins ne sont pas le facteur principal de la motivation, laquelle semble davantage contrôlée par le désir (Berridge 2004), même quand ce dernier est incompatible avec les besoins de l'individu (Berridge & Robinson, 2016). Le désir est lié à un état dans le cerveau, lequel est induit lorsqu'il y a prédiction et poursuite d'une récompense

(Berridge, 2004). Ces idées semblent montrer qu'il y a une discordance, c'est-à-dire une dissociation, entre besoin et désir, soit que les deux ne sont pas toujours synchronisés ; notamment que le besoin peut arriver sans qu'il y ait du désir et que le désir peut se produire en l'absence de besoin.

Concordance (association) entre besoin et désir

Toutefois, dans les théories économiques néoclassiques, la distinction entre besoin et désir est rejetée (McGregor et al., 2009 ; Morrow, 2015) ; et il est assumé qu'il n'y a « pas de désir sans besoin » (Dimen dans Feiner et al., 2005), cependant ces besoins/désirs peuvent avoir des niveaux d'urgences qui varient (Morrow, 2015). Ainsi, ces deux états sont souvent rassemblés sous le terme « utilité », c'est-à-dire l'un comme l'autre augmente l'utilité, soit la valeur des choses. Dans le même ordre d'idées, en neurosciences théoriques ou computationnelles, lesquelles utilisent des formulations mathématiques et des outils informatiques pour modéliser le fonctionnement du cerveau, la distinction entre besoin et désir n'est pas si importante puisqu'il est implicitement assumé que le besoin augmente automatiquement la valeur de la récompense, c'est-à-dire qu'il augmente automatiquement le désir (Zhang et al., 2009 ; Keramati & Gutkin, 2014 ; Niv et al., 2006 ; 2007 ; Friston, 2010 ; Parr et al., 2022). En d'autres termes, ces théories ne montrent que la concordance (association) entre besoin et désir, c'est-à-dire que les besoins et désirs sont synchronisés (du moins qu'il n'y a pas de besoin sans désir) ; et à partir d'elles il est difficile de comprendre la discordance (dissociation) entre besoin et désir, notamment la possibilité qu'il puisse y avoir besoin sans désir et l'inverse, comme discuté plus haut.

LIGNE DIRECTRICE

Il est important de se pencher sur l'hypothèse de la concordance (association) versus discordance (dissociation) entre besoin et désir. Elle permet de mettre au clair l'apparente contradiction

existante entre les différents courants de pensée, lesquels sont souvent implicites : « le besoin et désir sont deux choses différentes » et « le besoin et désir sont une même chose ». En effet, comme vu dans les deux paragraphes précédents, le besoin et le désir sont parfois en discordance (ou dissociation) et parfois en concordance (ou association). Dans cette thèse, je propose que les deux visions soient possibles, et que le besoin et le désir existent séparément, et qu'ils peuvent s'associer (concordance) tout comme ils peuvent être dissociés (discordance). La discordance entre besoin et désir est un indice qu'il y a au moins une différence entre les deux (cela n'empêche toutefois pas qu'il y ait des similitudes); et ainsi étudier cette différence pourrait permettre d'expliquer pourquoi parfois il y a discordance et parfois il y a concordance. Cette différence (et similitude) entre besoin et désir peut être appréhendée via des événements mesurables, c'est-à-dire leurs manifestations dans le comportement et dans le cerveau; ainsi que leurs natures (définitions) sur le plan théorique. En ce sens, nous verrons par la suite la différence entre les manifestations du besoin versus désir dans le comportement et dans le cerveau; et la différence de nature entre besoin et désir sur le plan théorique, notamment via les neurosciences théoriques. Ces différences, en particulier celle liée à leurs natures théoriques, permettront d'expliquer pourquoi il y a parfois discordance et concordance entre besoin et désir.

SUR LE PLAN COMPORTEMENTAL

Les expérimentations liées à l'aspect comportemental qui étudient la motivation procèdent souvent en mesurant le type, l'intensité et la quantité de réponse, réflexive ou volontaire, de l'humain ou d'autres animaux. Dans les prochains paragraphes, nous verrons comment le besoin versus le désir influence le choix et pourquoi, lorsque pris de manière isolée, le désir aurait, relativement au besoin, un plus grand impact sur la motivation dans son entièreté.

La motivation contient deux composantes : une directionnelle et une activationnelle

La motivation a un effet directionnel et un effet activationnel sur le comportement (Salamone et al., 2018). Il faut toutefois noter que, le comportement étant lié au système moteur (Swanson, 2000), la distinction entre aspects directionnel et activationnel, tels qu'ils sont abordés dans cette

thèse, concerne la portion somatique du système moteur (voir Swanson, 2000). C'est-à-dire celle liée au comportement externe et visible par les choix et les actions ; et non les subdivisions autonomes et neuroendocriniennes du comportement (voir Swanson, 2000). L'aspect directionnel de la motivation réfère au choix (préférence) d'action ou de stimuli (Salamone et al., 2018 ; Salamone, 1997, 2002 ; 2016), comme s'approcher de la nourriture ou éviter les choses nocives. L'aspect activationnel de la motivation concerne la vigueur : le haut niveau d'activité et la persistance qui caractérisent l'initiation et le maintien d'une action (Salamone et al., 2018 ; Salamone, 1992, 2016). Le désir dépend de la dopamine mésolimbique (Berridge, 1996) qui fournit à la fois un effet activationnel et directionnel (voir Salamone et al., 2018) et contrôle ainsi la motivation dans son entièreté. Tandis que le besoin, par lui-même, ne semble pas fournir l'effet activationnel que le désir fournit aux stimuli (Berridge, 2004 ; voir aussi Salamone et al., 2018), mais fournit un effet directionnel (Salamone et al., 2018 ; Balleine, 1992). En outre, si le désir et le besoin fournissent tous deux un effet directionnel aux stimuli, celui du désir est lié à la prédiction de la récompense ; et celui du besoin est pertinent en termes de conséquence sur l'état de l'organisme (Berridge, 2012 ; Balleine, 2009) ; et ces effets ne s'appliquent pas nécessairement en même temps selon les contextes.

Le désir contrôle la motivation, mais le besoin peut influencer la préférence en dehors du désir

En psychologie comportementale, on a pensé au départ que le besoin définissait la motivation, laquelle consistait à réduire le besoin (Hull, 1943). Toutefois cette idée a été abandonnée puisqu'elle ne pouvait pas expliquer que parfois, la motivation de faire une action augmente plus on la fait (Berridge, 2004). Aujourd'hui, on tend à admettre que le désir, « wanting » (vouloir), semble plus lié à la motivation et mieux l'expliquer que le besoin. Ce désir-vouloir est différent du désir comme souhait ou espérance (Berridge, 2012). Ainsi, pour le reste de la thèse, c'est à ce désir-vouloir que nous référerons par le terme « désir », par opposition à désir comme souhait ou espérance. La théorie qui explique la motivation via ce désir ('wanting') est celle de la saillance incitative (« incentive salience ») (Berridge & Robinson, 1998 ; voir également : Ikemoto & Panksepp, 1999 ; Salamone & Correa, 2002 ; Salamone, et al., 1997) qui stipule que le désir est basé sur deux processus neuropsychologiques : le premier est un signal qui prédit la récompense ; et le second est l'état dopaminergique (qui peut être influencé par les émotions, les

drogues, les besoins, etc.) (Berridge, 1996). Cette théorie s'est appuyée sur les travaux de Bindra (1974) qui avait montré qu'un stimulus qui signale la faim ne suscitait pas la motivation de manger, tandis qu'un signal lié à la nourriture menait à la motivation de manger, montrant que la prédiction de récompense contrôle plus la motivation que le besoin (Bolles et Moot, 1972 ; Berridge, 2004). Cependant, Toates (1994) a montré que le besoin tend à amplifier la motivation. C'est en ce sens que Berridge (1996) a utilisé les idées de Bindra et Toates dans un contexte de neurosciences et a lié leurs théories à la dopamine mésolimbique. Cette dernière octroie une saillance motivationnelle ou incitative (« incentive salience ») aux signaux qui prédisent la récompense et leur donne un pouvoir sur le comportement. Toutefois, il semble que le rôle du besoin dépasse celui d'amplificateur du désir. Balleine (1992) a montré que lorsqu'on utilise une nouvelle nourriture, l'état de faim a la capacité de donner la valeur à la nourriture et de contrôler cette valeur, et ce, par rapport à sa conséquence sur l'individu. De plus, il a été montré que la dopamine (DA) médie l'effort et la vigueur, mais que son absence ne réduit pas la préférence d'un stimulus lorsqu'on est dans le besoin (Salamone et al., 2018 ; Salamone et al 1997) ; ce qui indique une séparation entre le besoin et le désir dans la contribution sur les aspects directionnels et activationnels.

Résumé sur la portion comportementale

Pour résumer, le désir a un plus grand accès sur la partie activationnelle de la motivation, et donc sur le comportement, que le besoin. Lorsqu'il y a concordance, le besoin contribue à augmenter le désir et l'activation comportementale est amplifiée. Le désir et le besoin attribuent un effet directionnel aux stimuli, mais différemment. Pour le désir, les stimuli sont liés à la prédiction de la récompense et tiennent leur valeur (rôle) du fait qu'ils activent les comportements (comme dit plus haut, il s'agit ici de la portion somatique du système moteur [voir Swanson, 2000]). Pour les besoins, les stimuli sont pertinents à l'état actuel et tiennent leur valeur (rôle) du fait qu'ils apportent une conséquence positive sur l'organisme. Ces deux rôles attribuent la valeur aux stimuli, mais ne s'appliquent pas nécessairement en même temps selon les contextes, d'où la discordance. Ainsi, selon qu'il s'agit de besoin ou désir, la valeur du stimulus pourrait être représentée par différents patrons d'activation dans le cerveau (Dayan & Balleine, 2002 ;

Berridge & Aldridge, 2009). Cependant, cette dernière idée n'a pas été étudiée de manière approfondie dans l'optique de distinguer le besoin et le désir.

SUR LE PLAN DU CERVEAU ET DES NEUROSCIENCES

Pour différencier besoin et désir dans le cerveau, nous pouvons utiliser des méthodes d'imagerie cérébrale qui consistent à mesurer l'activité et la structure cérébrale liées à des comportements chez l'humain et chez d'autres animaux. Les données issues de ces méthodes permettent de décrire et de comparer les patrons d'activation entre différentes régions du cerveau, et ce, dans un état de besoin versus dans un état de désir.

Le besoin est lié à la prédiction intéroceptive, ainsi qu'à l'hypothalamus et l'insula

Comme les besoins sont liés à la privation de stimuli ou d'événements biologiquement significatifs, les régions cérébrales qui sont impliquées dans l'état de besoin, ou dans le traitement des stimuli dont on a besoin, sont reliées directement ou indirectement à l'hypothalamus (Sterling et Laughlin, 2015). En effet, ce dernier joue un rôle essentiel dans la coordination des réponses nécessaires à la survie de l'individu et de l'espèce (Swanson, 1987 ; Timbergen, 1951), ainsi que dans la surveillance de paramètres internes liés aux besoins de l'organisme (Sterling et Laughlin, 2015). Certaines des projections de l'hypothalamus vont vers l'insula (Allen et al., 1991 ; Dupont et al., 2003). Cette dernière joue un rôle important dans l'interoception, c'est-à-dire la perception des états internes. C'est en ce sens que l'insula est impliquée dans la prédiction intéroceptive, c'est-à-dire dans la représentation des états internes de l'organisme et celle de l'impact de stimuli externes sur ces états (Damasio, 2004 ; Naqvi & Bechara, 2010 ; Young & Nusslock, 2016 ; Menon et Uddin, 2010) ; et ce, même indépendamment d'une motivation ou d'un désir (Swanson, 2000). Ainsi, lorsqu'on a faim ou soif, l'insula mid-postérieure simule l'état de satiété futur en présence d'indices de nourriture ou

d'eau (Chen et al., 2016 ; Livneh et al., 2017 ; 2020 ; Barrett et Simmon, 2015) ; signalant un changement de prédiction intéroceptive (Livneh et al., 2017 ; 2020).

Figure 1

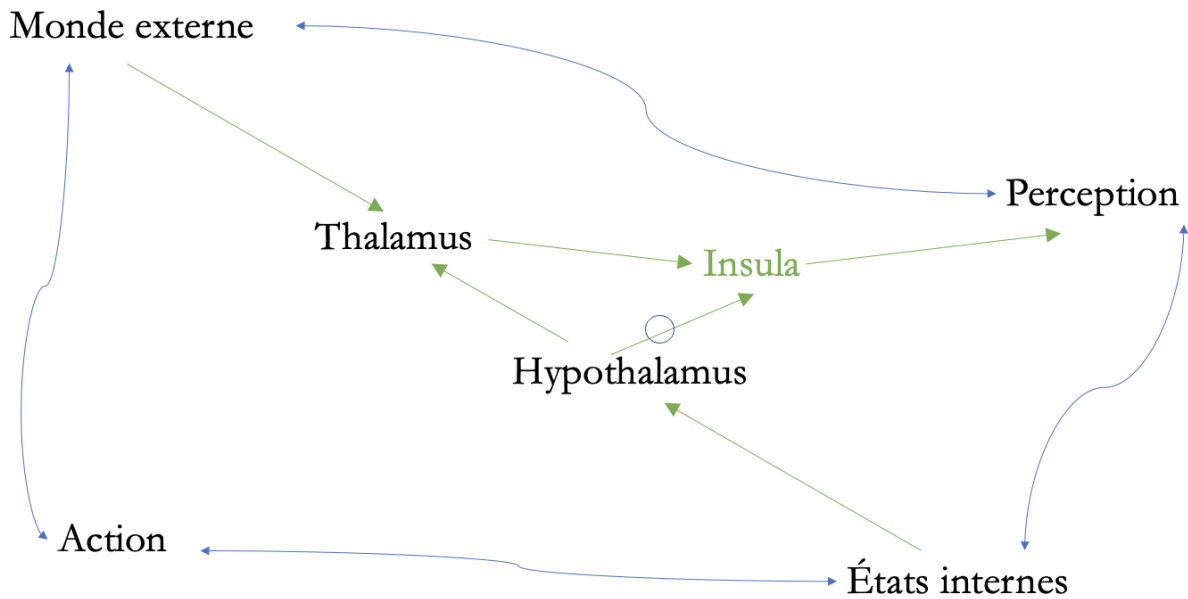


Schéma simplifié des régions discutées en lien avec l'état de besoin

Illustration des régions du cerveau ayant un rôle central dans la perception des états de besoin internes à l'organisme.

Peu de littérature sur les régions cérébrales communes aux besoins physiologiques et sociaux

Chez l'humain, les besoins ont plusieurs formes et peuvent être physiologiques (ex. : nourriture) ou sociaux (ex. : appartenance), etc. (Maslow, 1943 ; Baumeister & Leary, 1995 ; Maner et al., 2007). Or, peu d'études ont examiné le chevauchement entre les zones cérébrales traitant des besoins physiologiques et sociaux ; et quels neurotransmetteurs seraient impliqués. Une rare

étude en ce sens est celle de Tomova et al. (2020), qui a récemment montré un chevauchement en termes d'activations cérébrales entre la perception de nourriture et celle d'interactions sociales, lorsqu'on en est privé (donc dans un état de besoin), dans les régions de l'aire tegmentale ventrale (VTA) et de la substance noire (SN), des régions qui sont liées à la dopamine et donc au désir (voir la section suivante). Or, lorsqu'on regarde la littérature, l'insula, l'aire cingulaire antérieure (ACC) et le cortex orbitofrontal (OFC) semblent plus constamment activés autant pour les besoins physiologiques que sociaux (van der Lan et al., 2011; De Araujo et al., 2003 ; Mwilambwe-Tshilobo & Spreng, 2021 ; Tomova et al., 2020 ; Goldstone, et al., 2009 ; Vijayakumar et al., 2017) ; et donc la question de régions communes gagnerait à être étudiée plus en profondeur. Aussi, la sérotonine serait une bonne candidate comme neurotransmetteur lié au traitement global des besoins et des stimuli y étant associés, et ce, en dehors du désir (voir Sizemore, 2020). En effet, de faibles niveaux de sérotonine dans le cerveau signalent un état aversif (Dayan et Huys, 2009), ce qui caractérise aussi l'état de privation, et sont liés à une plus grande sensibilité à la nourriture (van Galen et al., 2021) et à une plus grande réactivité à l'exclusion sociale (Preller et al., 2015). À l'inverse, une hausse du niveau de sérotonine dans le cerveau indique à quel point l'état actuel est (ou devient) bénéfique (Liu et al., 2016). Cependant, bien que plusieurs études aient investigué les patrons d'activation respectifs du besoin et du désir, mis à part l'étude de Tomova et al. (2020), le chevauchement entre les zones cérébrales traitant des besoins physiologiques et sociaux a rarement été testé. De plus, comment le niveau de sérotonine pourrait être lié aux états de besoin n'a pas entièrement été élucidé. Il serait intéressant d'étudier les patrons d'activation cérébrale communs aux besoins physiologiques et sociaux pour des fins de généralisation ; et aussi d'explorer le lien entre ces zones cérébrales et la sérotonine.

Le désir est lié à la prédiction de récompense et à la réactivité du système de la dopamine mésolimbique

C'est la prédiction de récompense, et non la prédiction intéroceptive, qui contrôle le plus la motivation (Bindra, 1974 ; Bolles et Moot, 1972 ; Berridge, 2004). Les signaux qui prédisent une récompense déclenchent l'activité de la dopamine (DA) mésolimbique dans le VTA (Schultz,

1998 ; voir aussi Rice et al., 2010), qui projette ses neurones vers le striatum ventral (VS), notamment dans le noyau accumbens (NAcc) qui compose la plus grande partie du striatum ventral chez les primates (Haber & Knutson 2010), et qui énergise les actions pour obtenir la récompense (Li et Daw, 2011 ; Berridge et Aldridge, 2009 ; Lex et Hauber, 2008 ; Hamid et al., 2016 ; Zhang et al. 2009 ; Balleine et Killcross, 2006). Ainsi, le désir fournit à la fois une valeur directionnelle (choix dans le sens de la prédiction de récompense) et une valeur activationnelle (activation comportementale pour obtenir la récompense) (Hamid et al., 2016 ; voir aussi Salamone et al., 2018). Cela dit, le désir « vouloir » peut aller au-delà de la prédiction de récompense, et mettre dans un état où l'on peut faire des choses auxquelles on attribue moins de récompenses ou qu'on n'apprécie pas (Berridge, & Aldridge, 2009). Par exemple, les toxicomanes ont du mal à réduire ou à arrêter leur consommation de drogue même lorsqu'ils s'attendent à ce que ce soit moins gratifiant (Berridge & Robinson, 2016) ; et de la même manière, après avoir consommé un peu d'alcool, on peut faire quelque chose dont on attend que peu de récompenses. En effet, la décision d'agir est très influencée par la réactivité de la dopamine mésolimbique (Berridge, 1996), ainsi que celle du noyau central de l'amygdale (CeA) (Warlow & Berridge, 2021 ; Zhang et al. 2009 ; Balleine & Killcross, 2006). Ainsi, une réactivité de la DA mésolimbique ou du CeA trop élevée (induite par de la drogue, l'alcool, une émotion, un état de besoin, etc.) peut temporairement amplifier le désir bien au-delà de la valeur habituelle de la récompense (Tindell et al., 2005 ; Berridge & Aldridge, 2009) et mener à une recherche de récompense « irrationnelle » (Tindel et al., 2005 ; Berridge, & Aldridge, 2009). En outre, d'autres zones du cerveau contribuent d'une certaine manière au désir par leurs liens avec la DA la mésolimbique (VT et NAcc) notamment l'hypothalamus, le cortex ventromédian (vmPFC), plus précisément l'OFC et l'ACC, ainsi que l'amygdale basolatérale (BLA) ; le tout contribuant au système de la récompense (voir Haber & Knutson, 2010).

Figure 2

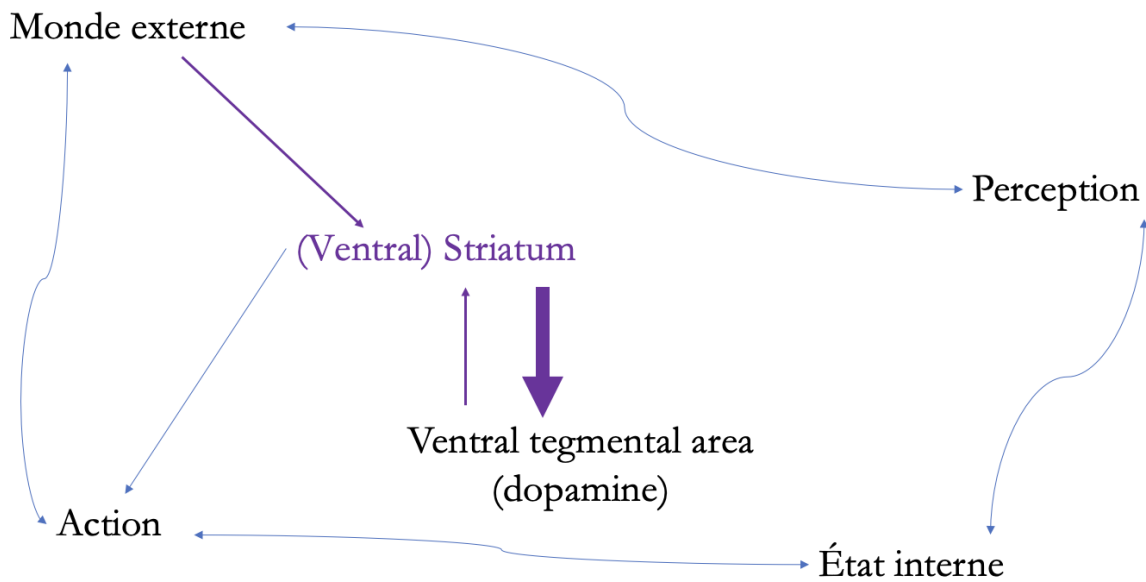


Schéma simplifié des régions discutées en lien avec l'état de désir

Illustration des régions du cerveau ayant un rôle central dans l'action induite par les états de désir.

Résumé sur la portion neuroscience

Pour résumer ce volet sur les manifestations des besoins et désirs dans le cerveau, et leur lien avec la discordance et concordance entre besoin et désir, il faut tenir compte non seulement des régions, mais aussi des types de prédictions liées à ces régions. Pour la manifestation du besoin dans le cerveau, les régions les plus importantes sont l'hypothalamus, qui semble être la source de l'état de besoin dans le cerveau, et l'insula, qui semble représenter l'état de besoin indépendamment du désir. Les régions les plus importantes du désir sont le VTA qui contient les neurones dopaminergiques qui s'activent lorsqu'il y a prédiction de récompense, et le NAcc qui a un grand impact sur l'activation du comportement. La discordance entre besoin et désir concerne aussi la fonction que jouent ces régions : les régions cérébrales qui médient le besoin semblent coder une prédiction interoceptive ; tandis que celles liées au désir médient la prédiction de récompense. La concordance entre besoin et désir viendrait de l'interconnexion entre les régions

cérébrales liées au besoin et désir ; ainsi que leurs connexions mutuelles avec d'autres zones du cerveau. La littérature concernant le désir a montré sa relation avec les régions de la dopamine mésolimbique, c'est-à-dire le striatum ventral et l'aire tegmentale ventrale (Haber & Knutson, 2010), tant sur le plan physiologique que social (Haber & Knutson, 2010 ; Berridge, 2009 ; Yousuf et al., 2018 ; Tomova et al., 2020 ; Spreckelmeyer et al., 2009 ; Rademacher et al., 2010 ; Hanewald et al., 2017). Il est ainsi pertinent d'examiner quantitativement le patron d'activation cérébrale, unique et commun aux besoins physiologiques et sociaux, et d'explorer leur relation avec un autre neurotransmetteur que la dopamine. De plus, on ne sait toujours pas clairement quel est le patron d'activation de l'état de besoin (physiologique et social) ni comment ce patron se différencie de celui du désir. Dans ce sens, il est intéressant d'élucider le patron d'activation cérébrale de la perception des stimuli pertinents lorsqu'il y a besoin sans désir ; et la perception des stimuli qui prédisent la récompense et donc créent du désir, sans qu'il y ait besoin.

SUR LE PLAN DE LA NATURE THÉORIQUE

Étudier la nature du besoin versus du désir nécessite un niveau d'abstraction plus élevé ; un niveau auquel la neuroscience théorique, plus communément appelée neuroscience(s) computationnelle(s), s'intéresse. Cette branche des neurosciences utilise des modèles mathématiques, des simulations sur ordinateur (*in silico*), ainsi qu'une théorisation du cerveau afin d'étudier les principes qui gouvernent le fonctionnement du cerveau (voir Trappenberg, 2010). Ici, nous utiliserons l'apprentissage par renforcement (Sutton & Barto, 2018) et l'inférence active (Parr et al., 2022), car ces approches ont en commun des éléments importants pour cette thèse. Il s'agit notamment de la notion d'état notée s , celle d'action notée a , et celle de « policy » notée π . L'état (s) représente une situation de l'environnement interne ou externe, et l'action (a) représente une manifestation qui modifie l'état actuel et aboutit à un nouvel état. Quant à elle, la policy (π) est un principe d'action adopté pour une situation (un état) donnée. Ici policy désigne à la fois une action individuelle basée sur un état donné, ou une suite d'état-action→état-action... ; et elle peut être émise par la créature ou par son environnement (voir Friston, 2020 ; Parr et al., 2022). Dans les deux cas, la policy représente

une séquence d'événements. La policy nous importe, car nous voulons distinguer comment le besoin versus le désir influence le choix ou attribue une valeur à des situations ou des stimuli.

Assumer la concordance ne permet pas de décrire clairement l'effet sous-jacent du besoin

Le désir dépend de la valeur des situations (états) selon qu'elles prédisent que la policy mènera à l'obtention de la récompense. En effet, l'architecture d'apprentissage par renforcement (telle qu'utilisée ici) a un fort lien avec la notion de désir, parce que l'état dans lequel l'agent se situe prédit les états et les récompenses futurs. Les études d'apprentissage par renforcement supposent souvent implicitement que les états de besoin augmentent la valeur de récompenses pertinentes (Niv et al., 2006 ; 2007 ; Zhang et al., 2009 ; Keramati & Gutkin, 2014). Parmi les exemples, Zhang et ses collaborateurs (2009) ont proposé un modèle computationnel et suggéré une variable représentant l'état dopaminergique, lequel dépend des états physiologiques (besoins, émotions, drogues, etc.), qui modifie la valeur de la récompense et augmente ou diminue le désir. Un autre exemple est le modèle computationnel de Keramati et Gutkin (2014), qui suggèrent que la valeur de la récompense est apprise et fixée de sorte qu'elle dépend de l'écart entre le point homéostatique actuel et celui optimal ; et cet écart représente l'état de besoin physiologique : plus il y a écart, plus la récompense prend ou perd de la valeur selon le sens de cet écart. Les propositions de Zhang et al. (2009) et de Keramati et Gutkin (2014) montrent deux facettes différentes de la concordance entre besoin et désir, et supposent implicitement que le besoin augmente automatiquement la valeur de la récompense, et donc le désir. Bien que semble logique puisque le désir a plus de contrôle sur les actions, il reste que ces théories font ainsi abstraction du mécanisme par lequel le besoin agit indépendamment du désir. Or, les états de besoin ont un effet sous-jacent non seulement sur le désir (Toates, 1994 ; Berridge, 2004), mais aussi sur le plaisir (Cabanac, 2017 ; Berridge & Kringelbach, 2015) ; mais surtout ils peuvent également influencer la préférence/choix ou la valeur des stimuli (Dickinson & Balleine 1994 ; Balleine, 1992) même en l'absence de l'activité dopaminergique (Wassum et al., 2011 ; Salamone et al., 2018), ou pousser à l'action ou à l'exploration même lorsqu'il n'y a pas de prédiction de récompense (Passingham & Wise, 2012 ; Panksepp, 2004). Cela indique que les états de besoins

biologiques ont un effet sous-jacent par lequel ils peuvent influencer certaines tendances vers des stimuli et actions nécessaires, et ce, indépendamment du désir.

L'origine de l'effet sous-jacent du besoin vient de la tendance à occuper des états préférés

Pour dissocier le besoin du désir, on peut examiner comment le besoin agit indépendamment du désir à travers l'inférence active (« Active Inference »). L'idée principale de cette théorie est que les organismes vivants obéissent à un impératif : minimiser la surprise de leurs observations sensorielles, c'est-à-dire de leurs états (Friston, 2010). Au sens statistique, la surprise mesure à quel point l'état actuel diffère de celui prédit. La minimisation de la surprise permet aux organismes vivants de résister (temporairement) à la deuxième loi de la thermodynamique, qui stipule que l'entropie — ou la dispersion d'un système — augmente toujours. En effet, l'entropie est la surprise moyenne et elle exprime l'incertitude liée à quel état doit être occupé. En ce sens, la présence d'un état avec forte probabilité réduit l'entropie. Par exemple dans le cas de la température optimale pour l'humain, qui est entre 36,1 °C et 37,2 °C ; attribuer une plus grande probabilité (à un humain) de se retrouver entre ces deux bornes de température réduit l'entropie ; puisqu'il y a désormais un état à occuper qui est prédit, et donc non surprenant. Ces états prédits peuvent être vus comme des états préférés innés (Parr et al., 2022 ; Friston, 2010) : les créatures vivantes ont évolué de sorte qu'elles ont une tendance à préférer naturellement les états les plus probables et limités qui maintiennent la vie (Parr et al., 2022 ; Sterling & Laughlin, 2015 ; Friston et al., 2006). Ainsi, lorsqu'on s'éloigne de l'état préféré et qu'on se retrouve dans des états surprenants, qui sont biologiquement coûteux, c'est-à-dire qui ont un effet négatif sur la survie de l'individu ; la tendance à occuper les états préférés génère un état de besoin, et active les polices pour y revenir. Les autres états (situations, actions, stimuli) qui se trouvent sur le chemin ou la trajectoire de ces polices prennent une valeur (Friston & Ao, 2012), et deviennent des stimuli (ou actions) dont on a besoin. Par exemple, pour passer de l'état de faim à l'état de satiété (préféré), un état intermédiaire est d'avoir de la nourriture ou de manger ; et cet état intermédiaire deviendrait valorisé parce qu'il est sur le chemin vers l'état préféré (satiété). C'est ainsi qu'une créature vivante expérimente le besoin de nourriture ou de manger, et cela même en dehors d'un stimulus qui prédit la récompense (nourriture), c'est-à-dire même en dehors du désir tel que défini ici.

La prédiction de récompense liée au désir est une précision sur la policy menant à la récompense

Pour comprendre comment cela diffère du désir, il faut voir, dans l'inférence active, la fonction de la dopamine, soit le neurotransmetteur central au désir (Berridge, 2007). Il a été démontré que la dopamine signale la croyance ou la confiance en la manifestation de la récompense (Lak et al., 2017 ; Gershman & Uchida, 2019) ; et cette confiance est statistiquement appelée précision (voir Parr et al., 2022). Dans l'inférence active, la dopamine représente la précision par rapport aux policies menant à la récompense (Parr et al., 2022 ; Holmes 2022). Autrement dit, la dopamine représente la confiance qu'une policy, émise par l'individu ou l'environnement, conduira à une récompense (Parr et al. 2022,). Ainsi, les stimuli qui augmentent la précision qu'une policy mène à la récompense déclenchent l'activation des neurones liés à la dopamine, qui attribueront une saillance incitative, c'est-à-dire du désir, à ces stimuli (Berridge 2007). D'où l'effet préparatoire de la dopamine mésolimbique (Cardinal et al., 2002) qui fait en sorte que l'individu soit prêt, c'est-à-dire s'active, à aller chercher ou à recevoir la récompense. C'est ainsi que le désir et la dopamine mésolimbique sont liés à la fois à la prédiction de récompense et à l'activation comportementale (Hamid et al., 2016). En ce sens, les signaux qui prédisent la récompense tirent leur force d'attraction et d'activation du fait qu'ils précisent la policy menant à la récompense.

Résumé sur la portion nature théorique

Nous avons ainsi la différence entre besoin et désir de par leurs natures. Le besoin est lié à la tendance à occuper des états préférés et à y revenir en suivant une policy ; et cela confère aux stimuli sur la trajectoire de cette policy une valeur de besoin. Tandis que le désir arrive lorsqu'un stimulus signale la précision sur la policy menant à la récompense. Cependant, l'influence directionnelle et sous-jacente du besoin séparément de la prédiction de récompense, c'est-à-dire du désir, n'a à ce jour pas été démontrée. Cela permettrait de séparer le besoin du désir, c'est-à-dire tester leur indépendance, et expliquer la discordance. Dans le même sens, il n'a pas été démontré comment cette même action directionnelle du besoin amplifie le désir, c'est-à-dire augmente la précision des signaux ou des récompenses qui mènent à l'état préféré ; ce qui expliquerait la concordance.

SECTION II : PROBLÉMATIQUE ET OBJECTIFS PRINCIPAUX

La problématique principale de cette thèse est d'étudier la différence entre le besoin et le désir afin d'expliquer la concordance et la discordance entre ces deux états. Dans l'introduction, trois domaines de distinction ont été évoqués : le plan comportemental, le plan de l'activité cérébrale et le plan de la nature théorique. Comme le désir a plus d'impact sur l'activation du comportement (dans la division somatique), dans cette thèse, c'est la différence sur le plan de l'activité cérébrale et celle sur le plan de la nature théorique qui seront abordées. Ces problématiques sont détaillées en trois points ci-dessous :

1. Il existe encore une certaine incertitude quant à savoir quelles régions peuvent être recrutées à la fois par le traitement des besoins physiologiques (ex. faim et soif) et sociaux (ex. exclusion/isolement) (mais voir Tomova et al., 2020 pour une première étude fMRI en ce sens). De plus, on peut se demander si et dans quelle mesure la sérotonine serait le neurotransmetteur qui médie la manifestation des états de privation et de satiété tant pour les besoins physiologiques que sociaux, c'est-à-dire des états de besoin généraux, à l'instar de la dopamine qui médie la manifestation des désirs. Cependant, une telle possibilité n'a pas été vraiment étudiée. **Par conséquent, la première étude présentée dans cette thèse vise à comparer chez l'humain les patrons d'activation cérébrale durant le traitement des stimuli physiologiques et sociaux dont on a besoin, afin d'identifier le patron d'activation cérébrale commun aux besoins physiologiques et sociaux et tester si ce patron est associé à la sérotonine.** Plus spécifiquement, nous identifierons quantitativement grâce à une approche méta-analytique les patrons d'activation cohérents pendant (ou après) l'observation de nourriture lorsqu'on a faim et d'eau lorsqu'on a soif ; ainsi que les patrons d'activation cohérents liés à l'observation d'une interaction sociale pendant (ou après) avoir été exclu de cette interaction. Nous comparerons ensuite directement ces patrons d'activation en

effectuant des analyses méta-analytiques de contraste et de conjonction pour respectivement identifier les similitudes et les différences entre les patrons d'activation des besoins physiologiques et sociaux. Le patron d'activation cohérent trouvé pour la conjonction des deux types de besoins sera utilisé pour tester la corrélation spatiale entre ces régions et la distribution des récepteurs de neurotransmetteurs, avec un intérêt particulier pour les récepteurs de la sérotonine.

2. Il n'est pas clair comment et quels patrons d'activation cérébrale contribuent de manière plus constante soit au désir, soit au besoin. Aussi, comme discuté, le cerveau attribue deux « rôles » (ou valeurs) différents aux stimuli liés aux états de besoin versus ceux liés au désir ; et ces deux rôles/valeurs ne s'appliquent pas nécessairement en même temps aux stimuli selon les contextes, d'où la discordance. Cependant, aucune étude n'a testé systématiquement la convergence de patron d'activation lié au besoin sans désir et celui lié au désir sans besoin. **Notre objectif pour la deuxième étude de cette thèse est donc d'utiliser une approche méta-analytique pour comparer les patrons d'activation cérébrale cohérents pour la perception des stimuli liés au besoin et celle des stimuli liés au désir, en identifiant les similitudes et les différences entre les patrons d'activation cérébrale de ces deux états.** Pour ce faire, nous identifierons quantitativement les patrons d'activation cohérents pendant (ou après) l'observation d'un stimulus alimentaire lorsqu'on a faim (besoin) versus après l'observation d'un stimulus prédicteur de récompense (désir). Nous comparerons ensuite directement ces patrons d'activation en effectuant des analyses méta-analytiques de conjonction et de contraste.
3. En théories économiques et en neurosciences computationnelles, les études supposent implicitement que le besoin augmente automatiquement le désir ; et par conséquent elles font abstraction du mécanisme par lequel le besoin agit indépendamment du désir. Or, les états de besoins biologiques ont un effet sous-jacent par lequel ils influencent certaines tendances vers des stimuli nécessaires pertinents qui se traduisent par l'amplification du désir, du plaisir, ainsi que le choix et la préférence indépendamment du (système du) désir. Cependant, la manifestation du besoin en dehors de ou en comparaison à la prédiction de récompense n'a jamais clairement été démontrée sur le plan computationnel

en tenant compte de la séparation entre besoin et désir. **L'objectif pour la troisième étude de la thèse est donc d'examiner conceptuellement comment les besoins orientent/dirigent le comportement (choix et sélection d'actions), même en l'absence du désir, et de tenter d'identifier le mécanisme par lequel cet effet directionnel influence le désir.** Pour ce faire, nous utiliserons une approche par modélisation afin de démontrer comment les états de besoin (états surprenants/biologiquement coûteux) influencent positivement la tendance à aller vers l'état préféré, même si cet effet n'est pas ou n'est que peu visible dans le calcul de la valeur de l'état ou de la combinaison état-action, qui est plutôt liée à la prédiction de récompense (et donc au désir). Nous utiliserons la même approche pour démontrer également comment cette tendance à aller vers l'état préféré fait que lorsque les états surprenants deviennent de plus en plus coûteux (état de besoin qui augmente), la présence d'un signal lié à la récompense qui mène vers l'état préféré réduit l'entropie et augmente la précision.

Les résultats des trois études présentées dans cette thèse, tant sur le plan des substrats neuronaux que sur le plan théorique, ont le potentiel de contribuer significativement à une meilleure définition et donc distinction entre le besoin et le désir. Ceci permettra également de mieux comprendre la discordance et la concordance entre ces deux états. Les données présentées dans cette thèse pourraient ultimement permettre de mieux comprendre pourquoi parfois nous choisissons des choses dont nous n'avons pas besoin ; ou qu'il arrive que nous ayons des besoins auxquels nous ne sommes pas motivés à répondre.

SECTION III : MÉTHODE ET HYPOTHÈSES

MÉTHODES LIÉES À L'IMAGERIE CÉRÉBRALE FONCTIONNELLE

Pour les deux premières études, l'approche sera d'utiliser les données issues des techniques d'imagerie cérébrale fonctionnelle, soient l'IRMf (Imagerie par résonance magnétique fonctionnelle) et la TEP (tomographie par émission de positons). Ces dernières sondent la corrélation entre les patrons d'activation cérébrale et la perception, cognition, ou la réponse comportementale du (de la) participant(e). Elles mesurent entre autres l'augmentation du rCBF (« regional cerebral blood flow »), qui est le flux sanguin qui accompagne l'activité des neurones dans différentes zones du cerveau. L'IRMf mesure indirectement le rCBF via le changement de niveaux d'hémoglobine oxygénée dans les zones cérébrales récemment actives, appelé « Blood Oxygenation Level Dependent » (BOLD), qui est détecté à l'aide de protocoles de résonance magnétique. Durant une expérimentation usuelle, le sujet est scanné dans la situation d'intérêt, puis dans une situation contrôle. Par exemple, pour mesurer l'impact de la faim sur l'activité du cerveau lors de la perception d'une pomme, on enregistrerait l'activité cérébrale de sujets lorsqu'ils regardent la pomme ; et ce, pendant qu'ils ont faim pour la situation d'intérêt ; comparé à pendant qu'ils sont satisfaits, pour la situation contrôle. Après avoir été standardisées (Talairach et Tournoux, 1988 ; Evans et al., 1992) et paramétrées (Friston et al., 1991 ; Worsley et al., 1992), les données recueillies peuvent être utilisées pour générer des données, issues de la différence entre la situation d'intérêt et la situation contrôle, et représentant les régions d'activation liées à la situation d'intérêt.

Il faut noter que les études de neuroimagerie ont souvent une faible réplicabilité, ou une flexibilité analytique et expérimentale différente, ou des échantillons de petite taille (Müller et al., 2018 ; Carp, 2012) ; et en raison du nombre d'études toujours croissant, il est difficile de suivre la richesse, mais aussi la variabilité des résultats (Radua & Mataix-Cols, 2012). Ainsi, il

est de plus en plus difficile de passer au crible l'énorme littérature sur la neuroimagerie, de trier parmi les résultats ceux qui sont reproductibles, et de les généraliser pour une même situation d'intérêt (Müller et al., 2018). Il est donc intéressant de combiner les résultats de plusieurs études qui sont faites sur une même situation d'intérêt afin de trouver, de manière quantitative, les zones cérébrales de convergence : celles qui sont consistantes entre les études. Ce genre d'évaluation s'opère via des méta-analyses. Les études méta-analytiques en neuroimagerie permettent entre autres d'étudier les patrons d'activation cérébrale liés à une situation (condition) donnée à travers différents paradigmes, échantillons et approches d'analyse, permettant d'obtenir un résumé quantitatif de la littérature existante (Müller et al., 2018). Ainsi, pour les deux premiers articles de cette thèse, des méta-analyses seront menées en utilisant l'approche d'estimation de la probabilité d'activation (activation likelihood estimate, ALE) (Turkeltaub et al. 2002 ; Chein et al., 2002) telle que révisée par Eickhoff et ses collègues (2009) (voir aussi Eickhoff et. al, 2012). La méta-analyse ALE prend en compte la variabilité intersujets et interlaboratoires généralement observée en neuroimagerie, et traite les régions d'activation en termes de probabilité : les régions où les différents résultats de la littérature convergent sont déterminées par l'union de probabilités de toutes les expériences incluses (voir Eickhoff, et. al, 2009 ; Eickhoff, et. al, 2012).

Plus précisément, des méta-analyses seront effectuées pour la première étude, afin de comparer chez l'humain les patrons d'activation cérébrale durant le traitement des stimuli physiologiques et sociaux dont on a besoin, et d'identifier le patron d'activation cérébrale commun aux besoins physiologiques et sociaux. Deux méta-analyses seront effectuées en solo pour identifier les patrons d'activation consistants pour, d'une part, les besoins physiologiques : faim/nourriture et soif/eau, activations pendant que les participants percevaient de la nourriture en ayant faim ou de l'eau en ayant soif ; et d'autre part, les besoins sociaux : exclusion (isolement)/interaction sociale ; activations lorsque les participants percevaient des interactions sociales tout en étant exclus (ou isolés) de cette interaction sociale. Pour repérer les régions communes à ces deux types de besoins, les résultats de ces méta-analyses en solo seront ensuite utilisés pour l'analyse des contrastes afin de différencier les deux conditions (besoins physiologiques et sociaux) ; et dans l'analyse de conjonction, pour identifier les régions cérébrales communément activées pour les besoins physiologiques et sociaux. Afin d'étudier le lien entre la manifestation commune de besoin dans le cerveau et la sérotonine, nous utiliserons une nouvelle approche développée par

Dukart et ses collègues (2021), qui permet de tester la corrélation entre les patrons d'activation mesurés par l'IRMf (incluant des données issues de méta-analyses) et la distribution spatiale des neurorécepteurs et transporteurs dérivée des mesures TEP. En d'autres termes, nous établirons une corrélation entre le patron d'activation cérébrale à la conjonction des « besoins physiologiques et besoins sociaux », et la distribution des neurorécepteurs, notamment ceux de la sérotonine. Dans cette étude, l'hypothèse principale est que les régions de l'insula, ACC et OFC sont parmi celles que nous retrouverons dans le patron d'activation commun ; et que ce réseau commun sera relié aux récepteurs de la sérotonine impliqués dans la sensibilité accrue envers les stimuli dont on est privé.

Des méta-analyses seront également effectuées pour la seconde étude, qui vise à comparer les patrons d'activation cérébrale cohérents pour la perception des stimuli liés au désir et celle des stimuli liés au besoin, en identifiant les similitudes et les différences entre les patrons d'activation cérébrale de ces deux états. Plus précisément, deux méta-analyses seront d'abord effectuées pour résumer quantitativement les résultats issus d'études en IRMf. Pour le besoin, il s'agira d'études IRMf dont la condition d'intérêt est liée à la perception d'un stimulus dont on a besoin : cartes d'activation prises lorsque les participant(e)s percevaient de la nourriture alors qu'ils(elles) avaient faim. Tandis que pour le désir, il s'agira d'études IRMf dont la condition d'intérêt est liée à la prédiction de récompense : cartes d'activation prises lorsque les participant(e)s percevaient un signal prédictif de récompense qui déclenche la recherche de récompense. Deuxièmement, nous effectuerons une analyse de conjonction pour identifier les régions communes qui sont constamment activées dans les deux états (besoin et désir). Enfin, les patrons d'activation du besoin et ceux du désir seront contrastés afin d'identifier les régions qui convergent différenciellement plus dans l'un des états que dans l'autre. Dans cette étude, nous nous attendons à ce que l'insula et l'hypothalamus puissent être plus activés pour le besoin et également retrouvés dans le contraste besoin moins désir ; et d'autre part, nous nous attendons à ce que les régions reliées à la dopamine mésolimbique, notamment le VTA et NAcc, soient constamment activées pour le désir, et davantage pour le désir que pour le besoin.

MÉTHODE LIÉE À LA MODÉLISATION COMPUTATIONNELLE

La troisième étude puise dans les techniques, théories et modèles des neurosciences computationnelles pour lesquelles les expériences sont souvent faites *in silico*, sous forme de simulation sur ordinateur. Dans cette étude, il y aura deux parties, la première concernant la nature de la motivation directionnelle que donne l'état de besoin, en dehors de toute prédiction de récompense. Statistiquement, cela est lié à une forme de tendance/probabilité élevée pour les états préférés comparés aux états surprenants, notamment lorsque les coûts biologiques sont élevés. La seconde concerne la manière dont cette motivation directionnelle (tendance) amplifie le désir (et le plaisir). Statistiquement, cela correspond à une réduction de l'entropie et augmentation de la précision plus l'état actuel devient surprenant/coûteux et qu'il y a un signal ou une récompense indiquant qu'on peut atteindre l'état préféré. Pour tester cela, nous effectuerons des simulations, en utilisant comme architecture l'apprentissage par renforcement, qui permet de modéliser comment un agent apprend à choisir les actions qui maximisent la récompense, selon l'état de l'environnement dans lequel il se trouve.

Rappelons-nous que les états préférés le sont parce qu'ils représentent des états physiologiquement viables qui sont limités. Ainsi, pour effectuer ces simulations, il faut un environnement où le nombre de possibilités de ce qui est biologiquement coûteux est disproportionnellement plus élevé que les quelques possibilités de ce qui est biologiquement viable. Ainsi, nous créerons un environnement dans lequel il y aura plusieurs états dont un seul sera l'état préféré (positif) ; tandis que les autres états seront plus nombreux et coûteux (négatifs). Dans notre cas, on peut se représenter cela par un monde sous forme de grille (grid-world) avec différentes cases, représentant des états dans lesquels on peut se trouver. Parmi ces états, un seul sera positif : l'état préféré. On peut faire un parallèle avec l'exemple de la température humaine : l'état préféré correspond à l'intervalle de température optimal (entre 36,1 °C et 37,2 °C). Dans cet exemple, cet intervalle représenterait un état (préféréd) et les autres nombreuses possibilités de température du corps seraient d'autres états (coûteux). Afin de tester les deux hypothèses, les coûts biologiques des états vont varier, sauf pour l'état préféré. En ce sens, pour la première question/hypothèse, le test consistera à voir si la variation des états de besoins/coûteux influence la tendance vers l'état gratifiant/préféréd. Pour la seconde question/hypothèse, il s'agit de tester si

la présence d'un chemin vers l'état préféré dans un environnement de plus en plus coûteux se traduit par une haute précision et une baisse d'entropie, comparativement à s'il n'y a pas un tel chemin vers l'état préféré. Pour les deux hypothèses, les coûts biologiques seront des récompenses négatives représentant un écart significatif par rapport à la valeur numérique de l'état préféré. Ces coûts seront gradués allant de -1, -10, -100, etc.

Pour la première question/hypothèse, deux agents seront générés, dans le même environnement décrit ci-haut. Les deux agents octroieront de la valeur à différents états, et le premier agent se limitera à ses prédictions de récompense pour choisir ses actions basées sur ses prédictions. Tandis que le second utilisera les valeurs d'états afin de calculer les probabilités de tendances à aller vers (ou à rester dans) l'état préféré versus les états surprenants, suivant l'hypothèse vue dans l'introduction. L'hypothèse est que plus les coûts biologiques augmentent (état de besoin), seule la préférence pour l'état menant à la récompense augmentera ; et cet effet sera plus visible pour l'agent 2 qui utilise des tendances que pour l'agent 1 qui utilise simplement des prédictions de récompense. Ceci suggérerait que le besoin a un effet sous-jacent et directionnel en dehors du désir, et que cet effet est lié à la tendance à occuper les états préférés. La deuxième hypothèse porte sur la manière dont la présence conjointe d'états coûteux (surprenants) et celle d'état préféré, ainsi qu'un chemin vers ce dernier, réduisent l'entropie et augmentent ainsi la précision. Afin de tester cette deuxième hypothèse, nous examinerons le changement de précision (l'inverse de l'entropie) qui provient de l'augmentation du coût biologique (surprise) lorsqu'il y a un signal de récompense (chemin vers l'état préféré) par rapport à l'absence de signal de récompense. L'hypothèse est que lorsqu'il y a des états de plus en plus coûteux (surprenants), la présence d'un chemin vers l'état préféré réduit l'entropie, et donc aura une plus grande précision. Ceci montrerait que le même effet sous-jacent du besoin lui permet de moduler le désir, lorsque le stimulus lié à ce désir réduit l'entropie en étant sur le chemin vers l'état préféré.

SECTION IV : RÉSULTATS PAR ARTICLES

RÉSUMÉS DE L'ÉTUDE 1

L'objectif de l'étude 1 était d'étudier les patrons d'activation cérébrale spécifiques et communs pour, d'une part, le traitement des stimuli physiologiques (faim et soif) et sociaux (exclusion sociale) dont on est privé/besoin. Pour atteindre cet objectif, nous avons utilisé une méta-analyse de neuroimagerie ALE, comparant des patterns d'activation cérébrale cohérents lors du traitement de stimuli pertinents (dont on est privé) dans des états de privation physiologiques et sociaux. Nous avons croisé les cartes des besoins physiologiques et des besoins sociaux pour identifier les zones cérébrales communes entre les besoins physiologiques et sociaux. À cet égard, nos résultats suggèrent que le traitement d'un stimulus physiologique et social dont nous sommes privés (c'est-à-dire dont nous avons besoin) semble tous les deux activer systématiquement l'insula postérieure, l'ACC pré-génuel et le noyau caudé. De plus, nous avons utilisé un modèle de corrélation spatiale afin d'identifier une relation possible entre ce réseau d'activation commun aux besoins physiologiques et sociaux et certains récepteurs de neurotransmetteurs en mettant l'accent sur les récepteurs sérotoninergiques. Notre analyse a montré que de tous les récepteurs de la sérotonine, le récepteur 5HT4 avait la corrélation la plus élevée. Cela suggère l'implication du récepteur 5HT4 de la sérotonine dans le traitement des stimuli dont on a besoin. Ainsi, il existe un réseau/pattern d'activation commun aux besoins physiologiques et sociaux, et de tous les récepteurs de la sérotonine, ce réseau est le plus corrélé au récepteur 5HT4.

CONTRIBUTION DES AUTEURS

Juvenal Bosulu : a conçu l'étude, effectué la recherche dans la base de données, effectué l'analyse et l'interprétation des données et rédigé le manuscrit. **Sébastien Héту** : a conçu l'étude, révisé le manuscrit et fourni des commentaires critiques. **Yi Luo** : a révisé le manuscrit et fourni

des commentaires critiques. Tous les auteurs ont contribué à la version finale du manuscrit et l'ont approuvée.

ÉTUDE 1 : COMMON BRAIN AREAS FOR PROCESSING PHYSIOLOGICALLY AND SOCIALLY 'NEEDED' STIMULI

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ABSTRACT

We looked at the overlap between brain areas related to perception of physiologically and socially (non-physiological) needed stimuli and how they might regulate serotonin levels. First, we conducted separate ALE meta-analyses on published results pertaining to brain activation patterns when participants perceived food while hungry or water while thirsty, and social interactions while being excluded. This allowed us to identify common consistent brain activation patterns for physiological and social needed stimuli. We also looked at significant spatial association between the common network and serotonin receptor distribution. We found that regions within the mid-posterior insula, the anterior cingulate cortex and the caudate are at the intersection of physiological (hunger and thirst) and social (exclusion) aspects of 'needing'. Furthermore, we found a significant positive spatial correlation between that common network and 5HT4 receptor among serotonin receptors. While this was the highest for serotonin receptors, it was not the highest of all receptors. Our study suggests there is a common brain pattern during the processing of physiologically and socially needed stimuli, and discusses their spatial association with serotonin receptors and its possible implication.

KEYWORDS: need, deprivation, meta-analysis, fmri, hunger, thirst, social exclusion, interoception, serotonin, neuroscience

INTRODUCTION

Needs are related to states of deprivation of a biologically significant stimuli or events (Bouton, 2016). They can be related to physiologically relevant stimuli and events such as food and eating for hunger, or water and drinking for thirst, but also to social stimuli and events like belongingness for social exclusion and meaningful social contact for social isolation (Maslow, 1943; Baumeister & Leary, 1995; Maner et al., 2007). Not responding to a need might lead to some adverse consequences such as physiological or psychological suffering which go beyond mere frustration (MacGregor 1960; Baumeister & Leary, 1995). Maslow (1943) (likely influenced by Hull's (1943) drive theory) was convinced that there are motivations which are driven by basic needs instead of external rewards. He ranked these needs which later became Maslow's pyramid. At the base, there are needs that are physiological, then needs of security, belonging, esteem, (more social needs) and actualization. When the lower order needs are satisfied to a certain extent, the higher ones appear gradually. Despite the fact that evidences seem to go against some definite hierarchy of needs both on an individual and on a societal level (Goebel & Brown, 1981; Hofstede, 1984; Tay & Diener, 2011), Maslow's ideas indicate that physiological and social needs have something in common: they have some negative effect if not met, and hence motivate people to choose stimuli (or actions) that satisfy them. Indeed, in the brain, physiological needs and social needs can both alter the affective value of their relevant/significant needed stimuli (Chen et al., 2016; De Araujo, 2003). It's important to stress that some social needs, such as social isolation, can have physiological effects almost similar to "true" physiological needs (Cacioppo et al., 2000; Tomova et al., 2020). Hence, in this study we focus on social needs that have less physiological effect, e.g. short term social exclusion. Indeed, the overlap between brain areas processing physiologically (e.g., through hunger and thirst) and socially (e.g., through short term social exclusion) needed stimuli have rarely been tested, especially on a meta-analytic level, which would provide a quantitative comparison of the processing of physiologically vs. socially needed stimuli.

The idea of needs can be considered to include two components : the state itself and the (needed) stimulus that alleviate that state. Since processing of the needed stimuli are more likely to control

behavior, either as cues or outcomes, than the deprivation states themselves (see Bindra, 1974; Toates, 1994), we will focus on brain responses associated with this processing. Hence, here we conceptualize the brain response to the perception of a stimulus, when deprived of it, as ‘needing’. For hunger and thirst, brain studies that measured brain response to (viewing, tasting, or smelling) food or (either ingesting drops of water or viewing beverages) while hungry or thirsty have reported activations in the insula (for hunger/food: van der Lan et al., 2011; Goldstone, et. al., 2009; Siep et. al., 2009; for thirst/water: De Araujo et al., 2003; Egan et al., 2003; Becker et al., 2017; Farrell et al., 2011), orbitofrontal cortex (OFC) (for hunger/food: van der Lan et al., 2011; Goldstone, et. al., 2009; Siep et. al., 2009; Führer et. al., 2008; for thirst/water: De Araujo et al., 2003; Saker et al., 2014), dorsal striatum (for hunger/food: van der Laan, et. al., 2011; Siep et. al., 2009), anterior cingulate cortex (ACC) (for hunger/food: Goldstone, et. al., 2009; Siep et. al., 2009; Führer et. al., 2008; for thirst/water: De Araujo et al., 2003; Becker et al., 2015, Becker et al., 2017; Farrell et al., 2011; Saker et al., 2013), amygdala and parahippocampal gyrus (for hunger/food: van der Laan, et. al., 2011; LaBar et. al., 2001; Führer, 2008; Goldstone, 2009; Mohanty, et. al., 2008; Chen et. al., 2020; for thirst/water: Becker, 2015), and posterior cingulate cortex (PCC) (for thirst/water: Farrell et al., 2011). Hence, although the brain networks supporting different types of physiological needs (here hunger and thirst) are not the same, they partially overlap in the ACC and amygdala, as well as OFC and the insular cortex; specifically the mid-posterior insula which has been shown to code for needed stimuli (see Bosulu et al., 2022; Livneh et al., 2020 ; Livneh et al., 2017). Furthermore, the insular cortex and ACC are viewed as common regions for conscious perception of both hunger and thirst (Mckinley et al., 2019), suggesting that they are core regions for homeostatic related perception and motivation (Craig, 2003).

Studies and meta-analyses of social exclusion/belongingness that have looked at brain responses to viewing others interact, or viewing (pleasant and/or close other) social stimuli while excluded from social interaction have reported activity in the ACC (Eisenberger, et al., 2003; Masten et al., 2009; Bolling et al., 2011; Vijayakumar et al., 2017; Mwilambwe-Tshilobo & Spreng, 2021), the posterior cingulate cortex (PCC) (Vijayakumar et al., 2017; Mwilambwe & Spreng, 2021); the insula (Masten et al., 2009; Bolling et al., 2011; Mwilambwe & Spreng, 2021), the ventral striatum (Masten et al., 2009; Vijayakumar et al., 2017), and the OFC (Cacioppo et al., 2013;

Vijayakumar et al., 2017). Overall, looking at these various results, social exclusion related responses to social cues/interactions seem to activate the insula, ACC, and OFC.

Overall, these different results suggest that brain networks supporting physiological and non physiological social needing at least partially overlap. Indeed, qualitatively the activation patterns of hunger/food, thirst/water, and social exclusion/belongingness often show activity within the insula (e.g. van der Lan et al., 2011; De Araujo et al., 2003; Mwilambwe-Tshilobo & Spreng, 2021; Tomova et al., 2020), ACC (ex. Goldstone, et. al., 2009; De Araujo et al., 2003; Mwilambwe-Tshilobo & Spreng, 2021) and OFC (ex. van der Lan et al., 2011; De Araujo et al., 2003; Vijayakumar et al., 2017). However, in a recent study directly testing for common brain areas when participants observed food versus social interactions, after respectively 10 hours of hunger or 10 hours of social isolation, only activations of regions containing mesolimbic and nigrostriatal dopamine neurons of the ventral tegmental area (VTA) and substantia nigra (SN) were found (Tomova et al., 2020). No study has compared physiological needs and social needs that have less physiological effect, such as short term social exclusion. Hence there is still some uncertainty with regard to if and which regions may be recruited by both the processing of physiological (hunger and thirst) and social needs (exclusion) that have less physiological effect. Hence, it seems timely to tackle this question using a meta-analysis which provides a quantitative analysis of the existing literature.

Tomova et al. (2020) study on hunger and social isolation seems to suggest that, because VTA/SN contain dopaminergic cell bodies, this neurotransmitter would be a neurotransmitter commonly involved in perception of physiologically and socially needed stimuli, likely turning deprivation into reward seeking for both types of needs. Beyond dopamine, we can wonder what other neurotransmitters might be related to the processing of physiological and social needed stimuli, especially for social needs that are not related to long term physiological process such as short term social exclusion. Serotonin is a good candidate for overall need processing, as it is central for biologically important sensory events (Sizemore, 2020). Indeed, low serotonin levels in the brain have been related to higher sensitivity to food (van Galen et al., 2021) and to higher reactivity to social exclusion (Preller et al., 2015). As low serotonin is often associated with aversive processing (Dayan and Huys, 2009) (which characterize deprivation); serotonin

secretion is said to indicate how beneficial the current state is (Luo et al., 2016; Liu et al., 2020). In that sense, (low) serotonin level might signal states of deprivation of both biologically and socially significant stimuli/events. However such a mechanism has not been elucidated.

Hence, the present study aimed at investigating the common and specific brain activation patterns for, on one hand, the processing of physiologically needed stimuli and on the other socially needed stimuli. As an exploratory objective, to help us understand how the brain processes relevant stimuli in a deprived state, we also tested for the spatial correlation between areas recruited during both the processing for physiologically and socially needed stimuli and brain regions associated with the spatial distribution of neurotransmitter receptors, with a specific interest in serotonin receptors, given its inherent link with well-being (see Luo et al., 2016; Liu et al., 2020).

METHODOLOGY

Meta-analysis of brain coordinate

We used a meta-analytic approach to quantitatively assess brain activation patterns of both physiological and social aspects of ‘needing’ using large collections of data. Meta-analyses make it possible to investigate questions across different paradigms, samples and analysis approaches. Specifically, we first conducted two meta-analyses to quantitatively summarize results from functional magnetic resonance imaging (fMRI) published studies on physiological needs: hunger/food and thirst/water (Physiological-Need); when participants perceived food while hungry or water while thirsty (that we will refer to as Physiological-Need) ; and on social non physiological need: short term exclusion/interaction; when participants perceived social interactions (that s/he was supposed to be part of) while being excluded from that social interaction (that we will refer to as Social-Need). These meta-analyses will help us look at brain regions that are consistently recruited for processing of either physiologically or socially needed stimuli. Second, we used the single meta-analytic results for contrasts analysis as well as a conjunction analysis to identify differences and overlaps in consistent brain activation for physiological and social ‘needing’.

We used the PRISMA framework and the following keywords to identify articles related to hunger: (“hunger” OR “food deprivation”) AND (“fMRI”). For thirst, we used: ("thirst" OR "water deprivation") AND ("fMRI"). For social exclusion, we used: ("social" AND "exclusion" AND "fmri"). Keywords were entered on PubMed (February 2021) for physiological needs and social needs. Additional articles were found by checking the articles references lists and review articles. For both physiological and social aspect of ‘needing’ the following inclusion criteria were used: healthy subjects; whole-brain analyses (with or without SVC), MNI or Talairach Coordinates (all Talairach coordinates were converted to MNI SPM152 in Ginger ALE using Lancaster transform; Lancaster et al., 2007); maps were corrected (or cluster level corrected); activation contrast only (see table 1 for selection criteria). The database returned 150 articles for hunger and 19 for thirst; 7 and 3 additional articles were found through other articles and reviews for hunger and thirst, respectively. In line with our objective, specific for physiological needs articles, we used two additional main criteria : 1) the participants were in a food or water deprivation state; 2) the participant was perceiving (visual, taste, odor, etc.) some food (while hungry) or water (while thirsty) stimulus. We found a total of 16 articles for hunger and 4 for thirst that met all inclusion criteria.

Regarding social exclusion/isolation, we found 129 articles, 22 were selected, and 4 more articles were found through other articles and reviews. Similarly to Physiological-Need, two additional main criteria were used for social needs : 1) the participant was in a social deprivationstate (i.e., s/he was either isolated from others or experienced social exclusion) ; 2) the participant was perceiving some social interaction s/he was excluded from. It’s important to note that these criteria resulted in all of our included articles for social needs using the cyber ball task (a virtual ball tossing game with other individuals from which the participant is excluded (Williams et al., 2000)), and were thus related to short term social exclusion. Social exclusion (as threat to fundamental social needs in humans) will cause emotional distress (Williams, 2007), and it has been proposed that the cyberball exclusion paradigm can induce need-like emotional distress (Bernstein and Claypool (2012). Based on these criteria and theories, we selected a total of 26 articles (for social exclusion) for the meta-analysis.

Meta-analyses were conducted with the activation likelihood estimation (ALE) approach using the Brainmap's GingerALE application. The revised ALE meta-analysis by Eickhoff and colleagues (2009) treats activation foci not as single point, but as spatial probability distributions centered at the given coordinates (Eickhoff et. al, 2012). It models spatial uncertainty by using an estimation of the inter-subject and inter-laboratory variability (typically observed in neuroimaging experiments). An ALE map is obtained by computation of union of activation probabilities for each voxel of all included experiments; and a permutation procedure is used to test for true convergence vs. random clustering (Eickhoff, et. al, 2012). The inference is done through the use of random-effects analysis that calculates the above-chance clustering between experiments. Furthermore, the algorithm gives more weight to gray matter compared to white matter by limiting the meta-analysis to an anatomically constrained space specified by a gray matter mask. For each single meta-analysis, we used the MNI152 coordinate system and the less conservative (larger) mask size. For hunger and thirst, there were 20 articles, 44 experiments, 856 subjects and 612 foci. (Hunger and thirst were merged together as physiological 'needing'). For social exclusion, there were 26 articles, 33 experiments, 1511 subjects and 342 foci. In our study, for main individual meta-analyses, all maps were thresholded using a cluster-level family-wise error (cFWE) correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ (uncorrected at the voxel level) (Eklund et al., 2016; Woo et al., 2014), and 1000 permutations. The contrasts analyses ([Physiological-Need] > [Social-Need] and [Social-Need] > [Physiological-Need]) compared the two different datasets (i.e. the ALE results from the Physiological-Need and Social-Need meta-analyses) for statistically significant differences, using the two cFWE corrected maps with $p < .01$ (uncorrected at the voxel level), 10,000 permutations (see Eickhoff et al., 2011). The conjunction analysis ([Physiological-Need] AND [Social-Need]), which is the main purpose of this study, was performed by intersecting the thresholded maps for physiological and social needs and allowed us to identify potential brain areas that were consistently activated during both physiological and social needs. Maps from meta-analyses were overlaid on a MNI template using Mango (<http://ric.uthscsa.edu/mango/>).

Spatial correlation with neurotransmitters

Using the conjunction results ([Physiological-Need] AND [Social-Need]) , we also looked at possible spatial (topographical) relationships between this intersection map and

neurotransmitters distribution whole-brain maps available in the JuSpace (as of december 2021). The latter is a MATLAB based toolbox introduced by Dukart and colleagues (2021) which allows for cross-modal correlation of spatial patterns of MRI or fMRI based measures with PET derived biological distribution of specific tissue properties, i.e. receptor density estimates covering dopaminergic, serotonergic, noradrenergic receptors and/or transporters (Dukart et al., 2021). A voxel-wise whole-brain family-wise error correction ($p < .05$ FWE corrected) was used for multiple comparisons (see Dukart et al., 2021). For the purpose of this study, we focused on serotonin receptors. Significant spatial association between subregions of the conjunction results and each neurotransmitter map were examined by comparing the distribution of z-transformed correlations (adjusted for spatial autocorrelation (i.e. adjusting for local gray matter probabilities as estimated from TPM.nii provided with SPM12)) against null distribution using one-sample t-tests (Dukart et al., 2021).

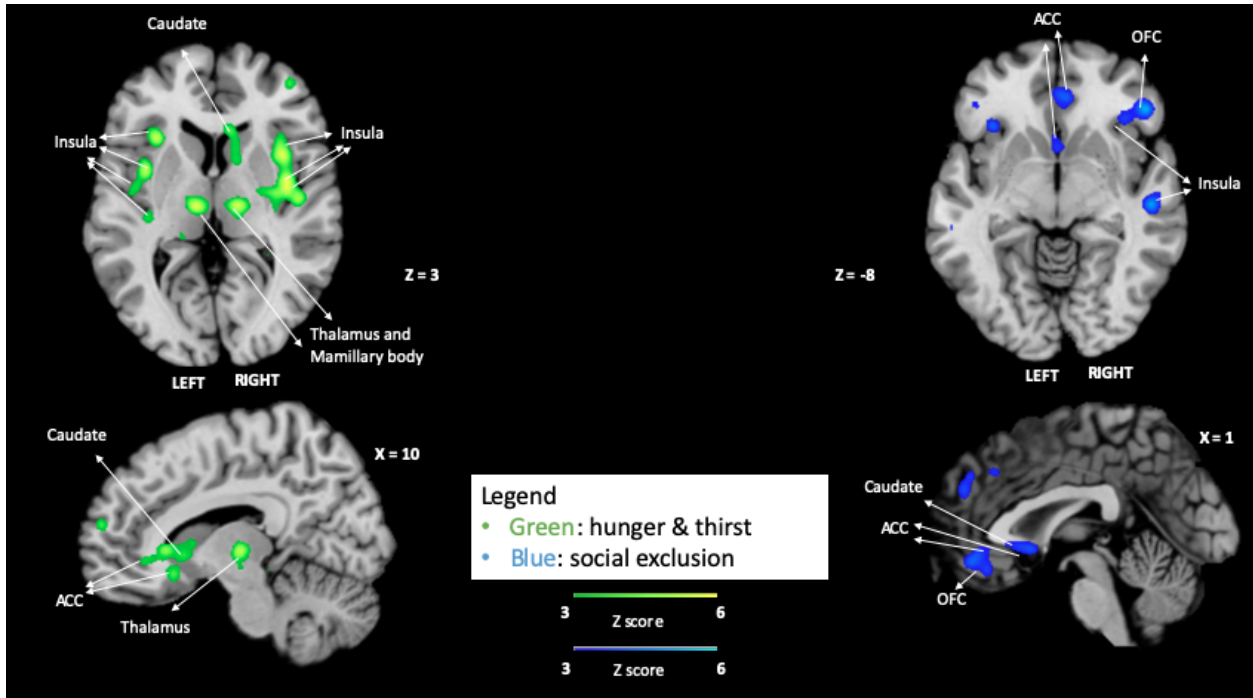
RESULTS

Single meta-analyses

The single meta-analysis on Physiological-Need, i.e. food and water perception during hunger & thirst (combined), revealed consistent activation within the following regions: the bilateral anterior insula, right middle insula, bilateral posterior insula, right claustrum, right putamen, bilateral ACC (B24 and B25), the bilateral caudate head, right caudate body, the left parahippocampal gyrus, the left medial frontal gyrus, right amygdala, right uncus, right mamillary body and right hippocampus (see figure 1).

The single meta-analysis on Social-Need, i.e. social interaction perception during/after social exclusion, revealed consistent activation within the right anterior insula, bilateral posterior insula, bilateral ACC (B24 and B32), right inferior frontal gyrus, right OFC, left anterior transverse temporal gyrus, and bilateral caudate head (see figure 1).

Figure 3



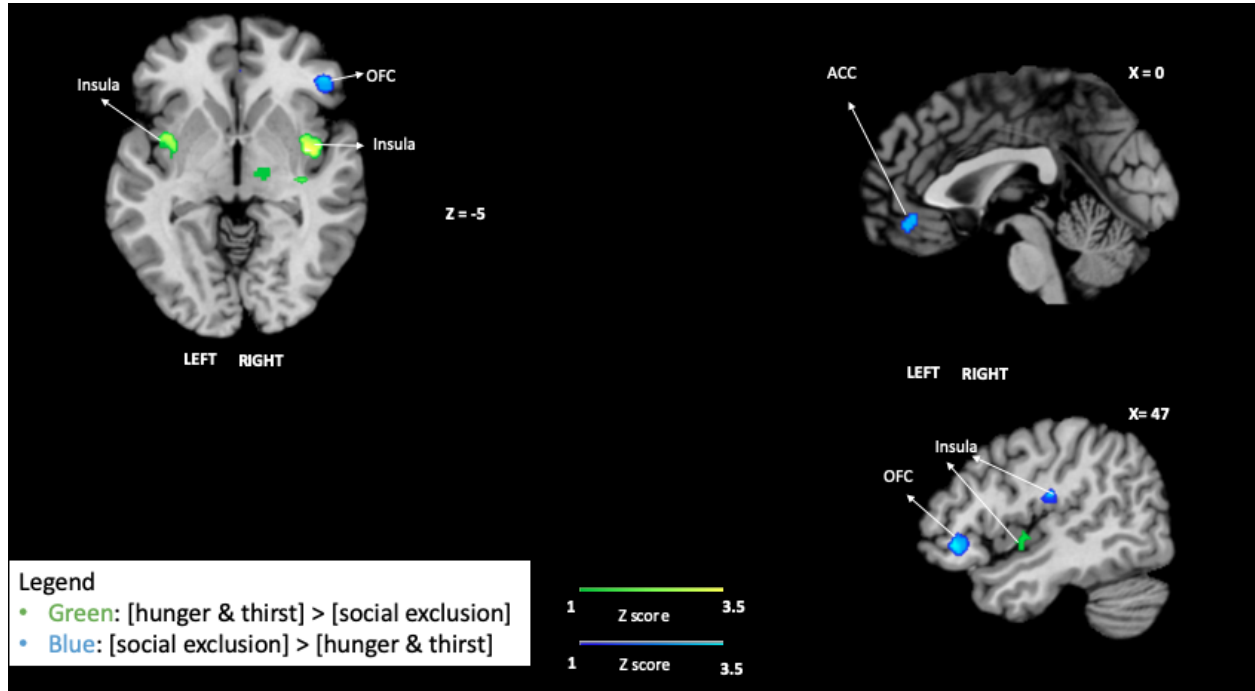
Single meta-analyses maps

Maps for activated clusters in each condition: Physiological-Need (green) and Social-Need (blue) and, showing activation patterns for each.

Contrasts meta-analyses

Contrasts meta-analyses results are summarized in figure 2. Compared to perceiving social interaction during social exclusion, perceiving food or water during hunger or thirst elicited more consistent activation within the bilateral posterior insula, right OFC and the bilateral caudate. Compared to perception of food or water during hunger or thirst, perception of social interaction during social exclusion elicited more consistent activation within the right posterior insula, the right OFC, right inferior frontal gyrus, and left ACC (B32).

Figure 4



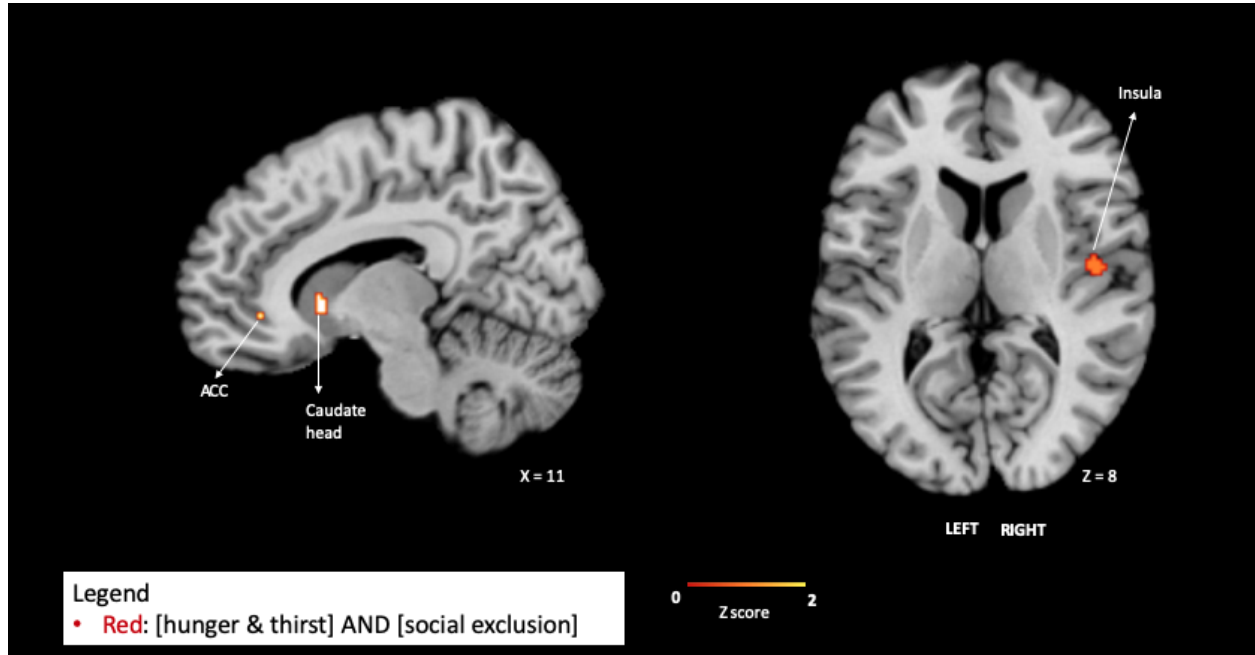
Contrasts maps

In green, clustered thresholded maps for clusters of subtraction {[Physiological-Need] minus [Social-Need]}. In blue, clustered thresholded maps for clusters of subtraction {[Social-Need] minus [Physiological-Need]}.

Conjunction meta-analysis

The intersection between [Physiological-Need] AND [Social-Need] showed overlapping consistent activation in the right posterior insula, right caudate head, and right ACC (B24). (see figure 3). It should be noted that the cluster size of the ACC, 8 mm³, is below what is usually used as minimum, i.e. 10 mm³.

Figure 5



Conjunction maps

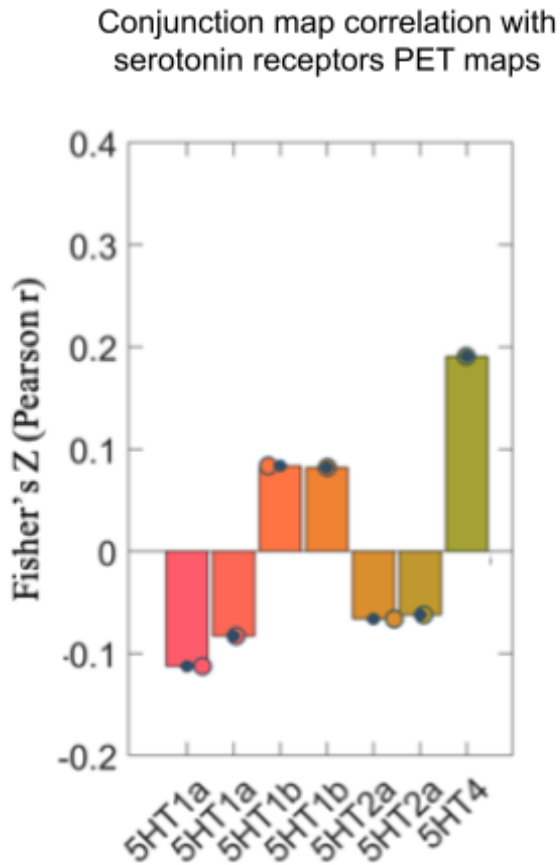
Clustered thresholded maps showing the intersection between activation patterns of [Physiological-Need] AND [Social-Need].

Spatial correlation between the conjunction map and serotonin neurotransmitter receptors

Finally, we also looked at the topographical relationship between brain coordinates found in our conjunction analysis [Physiological-Need] AND [Social-Need] and whole-brain maps of various neurotransmitters (with a focus on serotonin receptors) available in the JuSpace. Because (low) serotonin levels in the brain have been related to sensitivity to food (van Galen et al., 2021) and social exclusion (Preller et al., 2015), our focus was on serotonin receptors. Among serotonin receptors, significant positive spatial correlation between the regions showing consistent activation for physiological and social need and neurotransmitter maps were found for 5HT4 (see figure 4). Although this was the highest correlation with serotonin receptors, it was not the highest of all receptors (see supplementary material for full results). Regarding this, positive correlations were also found for : D1 and D2 dopamine receptors, DAT dopamine transporter, VAChT acetylcholine transporter, SERT serotonin transporter, 5HT4 and 5HT1b serotonin receptors, the Mu opioid receptor, mGluR5 metabotropic glutamate receptor. We found negative correlations for 5HT2a and 5 HT1a serotonin receptors, and CB1 endocannabinoid receptors.

This would indicate that dopamine, endogenous opioids, acetylcholine as well as serotonin neurotransmitters are spatially correlated with the intersection network.

Figure 5



Spatial correlation between the conjunction map and serotonin receptors

Error bars showing the Fisher's z Pearson correlation between the conjunction data on the y axis and the neurotransmitter map based on PET studies on the x axis. The colored dots represent data points and the black ones the mean of the bar which equals the to the single point.

DISCUSSION

Our goal was to investigate possible common and specific brain activation patterns for, on one hand, the processing of physiologically (hunger and thirst) and non-physiological socially (social exclusion) needed stimuli. To achieve this objective, we used ALE neuroimaging meta-analysis, comparing consistent brain activation patterns during processing of relevant (deprived) stimuli while in physiological vs. social deprivation states. We first carried out separate single meta-analyses on physiological ‘needing’ and on social ‘needing’. For perception of food and water in hungry and thirsty states, we found consistent activity within the insula, claustrum, putamen, ACC (B24 and B25), caudate head and body, the parahippocampal gyrus, the medial frontal gyrus, amygdala, uncus, mamillary body, and hippocampus. Perception of social interaction during social exclusion revealed consistent activation within the insula, ACC (B24 and B32), inferior frontal gyrus, OFC, anterior transverse temporal gyrus, and caudate head. We then contrasted those maps to identify differences. Compared to social ‘needing’, physiological ‘needing’ more consistently elicited activity within the putamen, claustrum, anterior insula, OFC, thalamus, mammillary body and amygdala. Compared to physiological ‘needing’, social ‘needing’ more consistently activated the posterior insula, the more lateral part of OFC, inferior frontal gyrus, and ACC. We also intersected the maps of physiological ‘needing’ and social ‘needing’ to identify common brain areas between physiological and social ‘needing’. In that regard, our results suggest that both processing a physiological and social stimulus we are deprived of (i.e. ‘needing’) seems to consistently activate parts of the posterior insula, ACC and caudate. Furthermore, we used the spatial pattern of that conjunction map in order to identify a possible relation between this common network and serotonin neurotransmitter receptors. Our analysis showed that of all serotonin receptors, the 5HT4 receptor had the highest spatial correlation. In the following paragraphs, we will discuss how these results can help us understand how the brain processes relevant stimuli in a deprived state.

Our single meta-analyses results are in line with the literature. Specifically, previous studies reported activation of insula and ACC for perception of food when hungry (van der Lan et al., 2011; Goldstone, et. al., 2009), water when thirsty (De Araujo et al., 2003), and social interaction when excluded (Mwilambwe & Spreng, 2021). Similar to these, we found consistent activation within the ACC and insula during perception of the physiologically and socially needed stimuli

in our single meta-analyses. In that sense, our results show that there is indeed an overlap between processing of physiologically needed stimuli and socially needed stimuli. The contrast [Physiological-Need] minus [Social-Need] revealed activation within the posterior insula, dorsal ACC, pregenual ACC, OFC, and caudate head, whereas the contrast [Social exclusion] minus [Hunger & thirst] did not include the caudate, but also revealed activation within the posterior insula, a more lateral part of the OFC and pregenual ACC. Our single and contrast meta-analyses suggest that neural populations treating physiologically and/or socially needed stimuli might be spatially closer (or even be the same) in the posterior insula and pregenual ACC. However, for other regions, (such as the OFC) that seem to be activated by both types of need when looking at a macro level, the activations are in different sub-regions when taking a closer look.

States such as hunger and thirst are referred to as homeostatic emotions (Craig, 2003). Despite how they are generated, homeostatic emotions have two important components : the aversive affect, and the affective motivation to terminate that affect (Craig, 2003). More specifically, thalamocortical projections provide both information about (1) the physiological condition of the body in interoceptive cortex at the dorsal and posterior part of the insula ; as well as (2) activation of limbic motor cortex, i.e., the ACC (Craig, 2003). These respectively generate the affective perception and motivation components (Craig, 2003). This is in line with our single meta-analysis results on hunger/food and thirst/water showing consistent activation within the posterior insula and the ACC.

Social exclusion has been said to activate the same dorsal region within the ACC as physical pain (Eisenberg, 2012). However, a recent meta-analysis of social exclusion with the cyberball task found a more ventral part of the ACC (Milambwe & Spreng, 2021). This latter result is similar to our single meta-analysis findings. So, it's possible that social exclusion and physical pain have slightly different brain activity patterns. Also, though social exclusion has been linked to activation of the anterior insula rather than the posterior insula (Eisenberg, 2012), our single meta-analysis on social exclusion found activity in both the posterior insula and in the anterior insula. This is in line with Milambwe & Spreng (2021) recent meta-analysis on social exclusion. However, Vijayakumar and colleagues (2017) did not find the insula in their social exclusion meta-analysis. The difference between our findings and Vijayakumar and colleagues (2017)

findings might be related to technical issues or inclusion criteria. Moreover, our study went further than the preceding meta-analyses by investigating the brain activation pattern between perception of social interaction while excluded and that of food/water when hungry/thirsty, enabling us to further assess the need aspect of social excursion in terms of brain patterns.

Some unanswered questions regarding need states might be hinted by looking at the common brain activation pattern map between psychologically and socially needed stimuli. Regarding this, our study shows that consistent brain activity patterns during perception of social interaction while being excluded partly intersects with that of perception of physiologically needed stimuli. This intersection was found within the posterior insula, ventral ACC and caudate which are related to aversive affects, affective motivation and goal directed behavior, respectively (Craig, 2003; Loonen & Ivanova., 2018; Balleine and O’Doherty, 2010). These three regions might be working in the following way: (1) An aversive affect perception of ‘needing’ is likely processed within the dorsal posterior insula (Craig, 2003), which integrates aversive emotional states and other homeostatic bodily functions (Gerlach et al., 2019) and likely signals a difference between actual and desired interoceptive state (Livneh et al., 2020; Barrett & Simmon, 2015). (2) The ACC contributes in facilitating directional motivation (Craig, 2003) possibly signaling the fulfillment of ‘needing’ as a requirement and distributing that signal to other brain regions (Weston, 2012) including the caudate (Peak et al., 2019). (3) Activation of the latter might indicate that perceiving needed stimuli leads to goal directed behavior and action choice (Balleine and O’Doherty, 2010; Knutson & Cooper, 2005; Hollon et al., 2014; Ito and Doya, 2015; Schwabe & Wolf, 2010), based on the current need (van den Bercken & Cools, 1982). Thus, our method and idea of looking at the common brain areas between psychologically and socially needed stimuli allowed us to further elucidate this mechanism. Following that, our findings suggest that perception of both physiologically and socially needed stimuli embed the affective perception, processed within the posterior insula, and the affective motivation toward the stimuli/event that terminates that need state, processed within the ventral ACC, which directs action choice within the caudate (Peak et al., 2019). Though this was initially suggested for homeostatic/physiological needs and their relevant stimuli (see Craig, 2003), our results lead us to suggest that this might be also true for social need states and social interaction.

As discussed in the previous paragraph, a possible link between social exclusion and hunger/thirst could be that they are both related to some displeasure/aversive state. This might also explain the inconsistency in the relationship between social exclusion and pain (Eisenberg, 2012; Milambwe & Spreng, 2021): social exclusion might be related, not to pain, but to displeasure. The latter is the inverse of pleasure (Cabanac, 2002) and as such includes, but is not limited to, pain. Indeed, displeasure can also be related to hunger, shortness of breath, disgust, depression, anxiety, fear, etc. (Becker et al., 2019; Berridge & Kringelbach, 2015) and is said to be processed within the pregenual ACC (and mesolimbic and amygdalar circuitry) (Becker et al., 2019), a region that we identified as being commonly recruited during both physiological and social needs.

It is possible that physiological needs and social exclusion share the negative feeling aspect of needing, and not as much the motivational aspect. Whereas, physiological needs and social isolation might share such a motivational aspect. Indeed, a recent study by Tomova and colleagues (2020) on the common brain areas between perception of food during hunger and social interaction after social isolation only found common activation within the substantia nigra (SN) and ventral tegmental area (VTA). These are dopaminergic regions, and the VTA mesolimbic dopamine has been linked to reward prediction, reward learning and motivation (Schultz et al., 1997; Schultz, 2015; Montague et al., 1996; Schultz, 1998; Rice et al., 2010; Hamid et al., 2016). However, in our conjunction analysis, which was about social exclusion rather than isolation, we did not find the VTA/SN nor the ventral striatum which receives VTA dopamine for action invigoration and reward seeking (Li and Daw, 2011; Berridge and Aldrige, 2009; Lex and Hauber, 2008; Hamid et al., 2016; Zhang et al. 2009; Balleine and Killcross, 2006). This is an indication that the difference between our findings and Tomova et al. (2020)'s is due to the difference between social exclusion and social isolation. This has been confirmed by other studies on social isolation (see Inagaki et al., 2016). However, it is important to note that not all studies on social isolation have found activity within the mesolimbic dopaminergic VTA or ventral striatum (see Cacioppo et al., 2009; D'agostino et al., 2019).

Our aim was to go beyond common brain activity patterns between psychologically and non-physiological socially needed stimuli, by running exploratory analysis to look at how these

common brain patterns—posterior insula, caudate and ACC—might be related to serotonergic receptors distribution in the brain. Our results show that at the conjunction regions between physiological and social ‘needing’, the serotonin receptor with highest density is the 5HT4 receptor. Our finding is in line with the suggestion that the 5HT4 receptor is a component of a feedback loop from the medial PFC to the dorsal raphe nuclei (DRN) (Rebholz, et al., 2018), specifically the prelimbic and infralimbic subregions (Peyron et al 1998, Lucas et al, 2005), which correspond to Brodmann areas 32 and 25 respectively (Price, 2007); which are part of the ACC (Weston, 2012). The ACC activity is related to both an affective motivation and an update of internal models, i.e. a feedback loop (Craig, 2003; Kolling et al., 2016; Petzschner et al., 2021). Some information from this feedback loop is said to be sent from the ACC to the dorsal raphe nucleus (DRN) (Rebholz et al., 2018; Lucas et al., 2005) which is the largest serotonergic structure in the brain (Liu et al., 2020). Our finding related to the spatial correlation between 5HT4 and the common brain map, leads us to suggest that this feedback loop can allow need states or needed stimuli to influence activity in the DRN through the ACC. That influence can be either inhibitory or excitatory via modulation of GABAergic (DRN inhibition) neurons and CB1 receptors (DRN excitation) in the DRN by the ACC (Lucas et al., 2005; Castello, et al 2018; Geddes et al.2016). Indeed CB1 has been found to be implicated in pleasure for both food (Kirkham, 2009) and social play (Achterberg et al., 2016). This might give some reason why needed stimuli are pleasurable. However we did not find much correlation between the common pattern map and CB1; suggesting that that CB1 actions could be further downstream, closer to the DRN rather than closer to the common brain map found in this study: posterior insula, pregenual ACC and caudate. Furthermore, though our findings did not show activity in the mesolimbic dopaminergic motivational areas, e.g. SN/VTA and ventral striatal activation; our finding, that the intersection network is correlated to 5HT4 distribution, could partly explain how needing, physiological or social needs can lead to activity within those areas. Indeed, the VTA/SN is modulated by DRN (Gervais & Rouillard, 2000), whose activity, as our study and literature suggest, is regulated by ACC via the 5HT4 receptor. In that sense: via 5HT4, pregenual ACC regulates the serotonergic DRN, which in turn can influence VTA/SN dopaminergic activity. In summary, our study suggests that the perception of a stimulus that would alleviate a negative physiological or social state (need) could be linked to brain regions that influence the activity of serotonin neurons.

LIMITS

The main limit of our study is that for physiological needs we only included hunger and thirst, while for social needs we only included social exclusion and not isolation. Nevertheless, it has been argued that both hunger and thirst implicate a similar network, that includes the ACC and insula (Mckinley et al., 2019), and the mechanism of that network is similar to other needs related to temperature, itch, visceral distension, muscle ache, ‘air hunger’, etc. (Crag, 2003). In the same way, social exclusion is different from social isolation: social isolation is more related to meaningful social contacts whereas exclusion is more related to being outcast of, or not able to participate in, some society (Huisman & van Tilburg, 2021)). Moreover, the contrasts of social exclusion included here are short term non physiological social needs, whereas social isolation is more long term, in terms of hours, and can have physiological impacts (See Tomova et al., 2020; Cacioppo et al., 2002). However they still have in common the fact that they refer to “lack of ties”, either with with society (exclusion) or with other significant persons (isolation) (Huisman & van Tilburg, 2021). Also, although there has been a debate between whether social exclusion actually causes need related distress (Gerber & Wheeler, 2009; Blackhart et al., 2009), Bernstein and Claypool (2012) found that Cyberball exclusion paradigm, used in this paper, may induce need-like emotional distress (e.g., reduced mood, and lowered self-esteem and other needs). Hence, the use of cyberball in this study is more coherent with a need state (Bernstein & Claypool, 2012). Future studies could assess a larger range of physiologically and socially needed stimuli, including those not included in the present study. Furthermore, one should not forget the limitations of reverse inference (Poldrack, 2006; 2011) in interpreting our results.

CONCLUSION

Our goal was to study the common and specific brain activations during physiological (hunger and thirst) and non physiological social (social exclusion) ‘needing’ as well as their relationship to the serotonergic system. Our results suggest that regions within the mid-posterior insula, the

ACC and the caudate are regions that commonly support processing/perception of both physiologically (hunger and thirst) and socially (exclusion) needed stimuli. So our result lead us to propose that ‘needing’ whether physiologically or socially is related to (1) an affective perception or response towards the needed stimulus that signal difference between actual and desired state, and which is processed within in the mid-posterior insula ; (2) an affective and directional motivation that requires the termination of the need state, processed within the ACC. (3) This requirement to terminate the need state facilitates goal directed behavior within the caudate. Furthermore, The network of regions at the intersection seem to be related to the distribution of receptors, and among the serotonergic receptors, the 5HT4 seem to have one the highest spatial correlation with that network. We hypothesize that, in need state and/or while processing the needed stimuli, this intersection network, through 5HT4, modulates DRN serotonin activity which signals how beneficial, or not, the current state is. In that sense, in the brain, physiological and social deprivation could lead to low serotonin levels, whereas the onset or presence of physiologically and socially needed stimuli could be related to high serotonin levels.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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AUTHOR CONTRIBUTION

Juvéanal Bosulu: Designed the study, performed the database search, performed data analysis, interpretation, and wrote the manuscript. **Sébastien Héту:** Revised the manuscript and provided critical feedbacks. **Yi Luo:** Revised the manuscript and provided critical feedbacks. All authors contributed to and approved the final manuscript version.

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RÉSUMÉS DE L'ÉTUDE 2

Le deuxième objectif était de comparer les patterns d'activation cérébrale liés à la valeur qui provient de de l'état de besoin versus l'état de désir. Pour répondre à cela, nous avons utilisé une méta-analyse de neuroimagerie ALE, comparant des patterns d'activation cérébrale cohérents lors du traitement des stimuli dans ces deux états. Nous avons utilisé la perception des stimuli alimentaires dans un état de faim comme modèle pour le besoin ; et la perception d'un stimulus prédisant une récompense pour le désir. Nous avons d'abord réalisé des méta-analyses distinctes pour chacun séparément, puis nous les avons croisées (conjonctions) et contrastées pour identifier les similitudes et les différences entre ces deux états. Nous montrons que le traitement d'un stimulus pertinent dans un état besoin semble plus lié à l'activité dans les cortex viscérosensoriels, c'est-à-dire l'insula mid-postérieure, et le putamen caudal-ventral (et dans une certaine mesure la queue du noyau caudé) ; et que le traitement d'un stimulus dans un état de désir semble plus lié à l'activité dans les zones cérébrales dopaminergiques mésolimbiques, les régions dopaminergiques nigro-striatales et les régions striatales et pallidales. Les deux états semblaient partager une activation cohérente dans le noyau caudé (tête et corps) et l'insula antérieure. Comparé au désir, le besoin a activé plus systématiquement l'insula postérieure médiane et l'ACC, le putamen caudo-ventral et la queue du noyau caudé, ainsi que

l'hippocampe. Comparé au besoin, le désir a activé de manière plus cohérente le système liée à la dopamine mésolimbique : le VTA et le striatum ventral et le pallidum, et les régions de dopamine nigrostriatale, c'est-à-dire SN et striatum dorsal. Les résultats de cette étude semblent montrer que les stimuli liés au besoin ont une valeur directionnelle, car ils influencent un changement de prédiction interceptive dans l'insula ; tandis que les stimuli liés au désir ont une valeur directionnelle, car ils prédisent un changement dans la prédiction de récompense via VTA et une valeur activationnelle sur le comportement via le striatum et le pallidum.

CONTRIBUTION DES AUTEURS

Juvenal Bosulu : a conçu l'étude, effectué la recherche dans la base de données, effectué l'analyse et l'interprétation des données et rédigé le manuscrit. **Sébastien Héту** : a conçu l'étude, révisé le manuscrit et fourni des commentaires critiques. **Max-Antoine Allaire** : a effectué la recherche dans la base de données, révisé le manuscrit et fourni des commentaires critiques. **Laurence Tremblay-Grenier** : a effectué la recherche dans la base de données, révisé le manuscrit et fourni des commentaires critiques. **Yi Luo** : a révisé le manuscrit et fourni des commentaires critiques. **Simon Eickhoff** : a révisé le manuscrit et fourni des commentaires critiques. Tous les auteurs ont contribué à la version finale du manuscrit et l'ont approuvée.

ÉTUDE 2 : 'WANTING' VERSUS 'NEEDING' RELATED VALUE: AN FMRI META-ANALYSIS

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ABSTRACT

Consumption and its excesses are sometimes explained by imbalance of need or lack of control over ‘wanting’. ‘Wanting’ assigns value to cues that predict rewards, whereas ‘needing’ assigns value to biologically significant stimuli that one is deprived of. Here we aimed at studying how the brain activation patterns related to value of ‘wanted’ stimuli differs from that of ‘needed’ stimuli using ALE neuroimaging meta-analysis approaches. We used the perception of a cue predicting a reward for ‘wanting’ related value and the perception of food stimuli in a hungry state as a model for ‘needing’ related value. We carried out separate, contrasts, and conjunction meta-analyses to identify differences and similarities between ‘wanting’ and ‘needing’ values. Our overall results for ‘wanting’ related value show consistent activation of the ventral tegmental area, striatum and pallidum, regions that both activate behaviour and direct choice; while for ‘needing’ related value we found an overall consistent activation of the middle insula and to some extent the caudal-ventral putamen, regions that only direct choice. Our study suggests that wanting has more control on consumption and behavioral activation.

INTRODUCTION

Current consumption (e.g. food, transport, etc.) in western countries seems to be one of the causes of ecological problems we are facing (Lipschutz, 2001). According to some, this consumption is in part due to the fact that we consume what we want beyond what we need (Stearn, 2006). Apart from problems related to ecology, in our daily behaviors such as those

related to food consumption, excesses and maladaptive behaviors are sometimes explained by an imbalance of need or a lack of control over ‘wanting’. Indeed, Campbell (1998) reports that research on consumer behavior has shown that there are two types of rhetoric used to justify the action of purchase: needs and wants, as well as their synonyms. He also argues that rhetoric of needs is derived from utilitarianism and puritanism that advocated a life based on necessity or satisfaction; while the rhetoric of wants is based on romanticism and linked to the pursuit of pleasure (Campbell, 1998). Beyond this rhetorical distinction, one can wonder: is there a true difference between something that we need and something that we want? At the neural level, needing is related to a state of deprivation of something important for life or survival (Bouton, 2016), and increases arousal through interoceptive salience (Craig, 2003). ‘Wanting’ is related to the prediction of reward in the brain and is more closely related to motivation (Berridge, 2004). Although earlier theories suggested that need or deprivation defines motivation (Hull, 1943), it was later demonstrated that cues that signal hunger do not elicit motivation to eat, while food-related cues did lead to motivation to eat (Bindra, 1974), showing that motivated behaviours are more determined by reward prediction (which is closer to ‘wanting’) than need state, though the later can have multiplicative effect (Toates, 1994). The distinction might seem clear. However, since ‘needed’ stimuli are often pursued and thus associated with motivational value, it’s not obvious whether an external stimulus, such as food, is pursued because of its ‘needing’ or ‘wanting’ related value. As ‘needed’ stimuli might have a different form of value than ‘wanted’ stimuli, we can wonder how in the brain the value of ‘needed’ stimuli differs from that of ‘wanted’ stimuli.

Given that we cannot test wanting and/or needing as general phenomena, here we are testing some manifestation of them. Hence, to conceptualize this distinction, we refer to “wanting a stimulus” as ‘Wanting’_{ST}, which represents a brain reaction to a reward predicting cue that triggers reward seeking. We refer to “needing a stimulus” as ‘Needing’_{ST}, which represents the brain reaction to a stimulus that one is deprived of, without necessarily seeking it. We propose to use activation pattern to the perception of a cue predicting a reward as a model for ‘Wanting’_{ST} related value; and to use the activation pattern during the perception of a food stimulus while in the state of hunger as a model for ‘Needing’_{ST} related value (Silverman et al., 2014; Spear, 2011). In order to answer our question, we used a neuroimaging meta-analytic approach, comparing the

patterns of brain activations during the processing of ‘Wanting’_{ST} versus ‘Needing’_{ST}. Previous meta-analyses have focused on either ‘Wanting’_{ST} (Wilson et al., 2018; Oldham et al., 2018; Sescousse et al. 2013) or ‘Needing’_{ST} (van der Lan et al., 2011; LaBar et al., 2001; Chen & Zeffiro, 2020), but no work has directly compared both activation patterns.

‘Wanting’_{ST} related value

Non-human animals tend to respond and ‘want’ food even when they are no longer hungry (Bouton, 2016). This is also the case for humans: cues of M&M or pictures of cigarettes (for smokers) lead to more consumption even after having been consumed to satiety (Watson et al., 2014; Hogarth & Chase, 2011). ‘Wanting’_{ST} is a concept from incentive salience theory that comes from animal studies (Berridge & Robinson, 1998; see also: Ikemoto & Panksepp, 1999; Salamone & Correa, 2002; Salamone, et al., 1997) which states that ‘Wanting’_{ST} is based on two neuropsychological processes: the first is a pavlovian cue that predicts the reward; and the second is the dopaminergic state (which might be enhanced by hunger, thirst, emotions, drugs, etc.) (Berridge, 1996). In other words, ‘Wanting’_{ST} depends on external stimuli that act as pavlovian cues that predict rewards (Berridge, 2018). The attribution of value to these cues depends on mesolimbic dopamine (Berridge, 1996). The latter is secreted within the ventral tegmental area (VTA) by a reward cue (Schultz, 1998), and projected within the nucleus accumbens (NAcc), ventral pallidum, and on the central amygdala opioid (Warlow & Berridge, 2021; Zhang et al. 2009). In this sense, the VTA would be more related to reward prediction (Schultz, 2015; Schultz et al., 1997) and its phasic activation determines directional value (preference/choice or action selection), while the NAcc is more related to value attribution (an incentive salience) to that reward prediction (Berridge and Aldrige, 2009; Lex and Hauber, 2008; Hamid et al., 2016), along with the central nucleus of the amygdala (Warlow & Berridge, 2021; Zhang et al. 2009; Balleine & Killcross, 2006). Thus, ‘Wanting’_{ST} starts with reward prediction. Human studies on reward prediction have shown the involvements of the orbitofrontal cortex (OFC) (O’Doherty et al, 2002; O’Doherty, 2004), VTA (O’Doherty et al, 2002; Krebs et al., 2009; Carter et al., 2009; Schott et al., 2008; Oldham et al., 2018), NAcc and ventral striatum (O’Doherty et al, 2002; Knutson et al 2003; O’Doherty, 2004; Knutson et al 2001; Wilson et

al., 2018; Carter et. al., 2009; Schott et. al., 2008; Oldham et. al., 2018; Simon et. al., 2015), amygdala (O'Doherty et. al, 2002; O'Doherty, 2004; Oldham et. al., 2018) and insula (O'Doherty et. al, 2002; Wilson et al., 2018; Oldham et. al., 2018). These results suggest that, in humans, the activation pattern of reward prediction which leads to 'Wanting'_{ST} related value could implicate these regions.

'Needing'_{ST} related value

A need state has the capacity to give and to control the preference/choice related value of a novel food or drink in relation to its consequence on the organism, once the organism has experienced the benefit of that stimulus in the need state (Dickinson & Balleine 1994; Balleine, 1992). Thus, 'Needing'_{ST} related value can have an impact on choice and action selection (Dickinson & Balleine 1994) or preference (Salamone et al, 2018). For instance, hunger influences flavour preference learning in humans based on flavour (Brunstrom & Fletcher, 2008; Zellner et al., 1983), nutrients (Gibson et al., 1995; Kern et. al, 1993; Appleton et al., 2006), and odour-sweetness (Yeomans & Mobini, 2006). Moreover, the shifts in preference are found to persist beyond the initial training period (Brunstrom & Fletcher, 2008), suggesting a long term learned value. However, though 'Needing'_{ST} provides directional value (preference/choice or action selection), in absence of reward prediction, 'Needing'_{ST} (by itself) does not activate behavior (Bindra, 1974; Toates, 1994; Bolles and Moot, 1972; Berridge, 2004). In the brain, it has been suggested that 'Needing'_{ST}, which depends on interoception and its prediction and its prediction error (i.e., difference between predicted need state and actual need state) within the anterior insula and mid-posterior insula, respectively (Barrett & Simmon, 2015), also often recruits the anterior cingulate cortex (ACC) (Craig, 2003). Moreover, 'Needing'_{ST} related value attribution implicates the OFC (Ostlund and Balleine, 2007; Balleine & O'Doherty, 2010), while 'Needing'_{ST} related learning recruits the basolateral amygdala (Balleine and Killcross, 2006) and the long term association between external stimuli and their consequence on physiological need states recruits the caudate body and tail as well as the putamen, mostly the caudal-ventral putamen (Seger & Cincotta, 2005; Schwabe & Wolf, 2010; Kunimatsu et. al., 2019; Amita, et. al., 2018), and insular cortex (Balleine and Dickinson, 2000). Overall, previous fMRI meta-analyses and studies on hunger in humans have revealed regions associated with sensory

integration, reward processing, and taste; including the insula (van der Lan et al., 2011; Goldstone, et. al., 2009; Siep et. al., 2009), the OFC (van der Lan et al., 2011; Goldstone, et. al., 2009; Siep et. al., 2009; Führer et. al., 2008), the amygdala (van der Laan, et. al., 2011; LaBar et. al., 2011; Führer, 2008; Mohanty, 2008; Goldstone, 2009), the dorsal striatum (van der Laan, et. al., 2011; Siep et. al., 2009), and the ACC (Goldstone, et. al., 2009; Siep et. al., 2009; Führer et. al., 2008); and many studies have found activations within the amygdala/parahippocampal gyrus (LaBar, et. a., 2011; Mohanty, et. al., 2008; Chen & Zeffiro, 2020). Hence hunger can cautiously be used as a proxy for 'Needing'_{ST}. Thus, based on the inherent association between hunger (and thirst) and 'Needing'_{ST}, the insula and ACC, and to some extent the OFC, amygdala, and caudate may be engaged in the processing of 'Needing'_{ST} related value and contribute to directional value.

Two types of predictions and values

The conceptualization of 'Wanting'_{ST} and 'Needing'_{ST} here as processing of either wanted or needed stimuli implies two forms of predictions. Indeed, in both cases, the value of stimuli often depends on a prediction and a prediction error: in case of 'Wanting'_{ST}, that prediction is related to reward (unexpected reward or reward predicting cue) and is computed in the ventral striatum (Takahashi et al., 2016), while the prediction error is computed in the VTA (Schultz, 2015). For 'Needing'_{ST}, that prediction is related to interoception (predicted state vs sensed state) and is said to be computed in visceromotor cortices (OFC, ACC, anterior insula), whereas the interoceptive prediction error is proposed to be computed within the mid-posterior insula (Barrett & Simmons, 2015). Moreover, both 'Wanting'_{ST} and 'Needing'_{ST} establish a relation between the state ('wanting' state and 'needing' state) and some external stimuli, where the state attributes some form of value to the stimuli. The value assigned to stimuli (by both 'Wanting'_{ST} or 'Needing'_{ST}) can have a directional effect or activational effect. The directional effect is linked to choice (preference or action selection) and directs towards or away from stimuli, while the activational effect is related to action and its initiation, maintenance, and vigor or effort (see Salamone et al., 2018). Indeed, 'Wanting'_{ST} depends on mesolimbic dopamine (Berridge, 1996) which provides full motivational value to reward as it provides both activational value (or effect) and directional value (or effect) to stimuli (see Salamone et. al., 2018). 'Needing'_{ST} (by itself) doesn't seem to provide the activational value that 'Wanting'_{ST} provides to stimuli (Berridge, 2004; see also

Salamone et al., 2018). However, ‘Needing’_{ST} do provide directional value (Salamone et al., 2018; Balleine, 1992). Importantly, if both ‘Wanting’_{ST} and ‘Needing’_{ST} provide directional related value to stimuli that impacts choice, they do so in different ways. In the case of ‘Wanting’_{ST}, that choice value is pavlovian cue triggered and stimulus related (Berridge, 2012 ; Balleine, 2009). In the case of ‘Needing’_{ST}, that choice value is act-outcome based (Balleine, 2009). Hence, depending on either state, stimulus value could be represented by different activation patterns in the brain (Dayan & Balleine, 2002; Berridge & Aldridge, 2009). However, no work has quantitatively tested this hypothesis.

Although ‘Wanting’_{ST} takes both cues and physiological states, and the latter can be related to need states (Berridge, 1996; Zhang et al., 2009), not all physiological states are related to needs, some are related to emotions, drugs etc. (Berridge, 1996; Zhang et al., 2009). Moreover, need states can give and control value to relevant rewards in relation to their outcome by associating the discriminative properties of needs with the increased value placed on the reward (Nader et. Al., 1997; Balleine, 1992), and such ‘directing’ motivational control through determination of specific outcome values is said to be dopamine independent (Niv et al., 2006; Balleine, 2005; see also Salamone et. al., 2018). We believe there is an objective reaction to stimuli that are needed, even in absence of an incentive salience motivation, i.e. ‘Wanting’_{ST}. In the same way there is an objective reaction to ‘Liking’_{ST} in absence of ‘Wanting’_{ST} (see Berridge, 1996); and in the same way there is an objective ‘Wanting’_{ST}, that can happen regardless of ‘Needing’_{ST} or ‘Liking’_{ST} (see Berridge, 2004). Regarding the difference between ‘Wanting’_{ST} vs ‘Needing’_{ST}, they likely provide two different “roles” (or values) to reward cues. We believe that, depending on situations or paradigms, ‘Wanting’_{ST} related cues are stimuli that motivate action and bias behavior (see Robinson et al., 2014); whereas the Needing’_{ST} related cues are stimuli that are outcome-relevant for the current need state (see Balleine, 2005); and our view is that those two roles/values don’t necessarily apply at the same time to stimuli depending on situations/paradigms. Our study is thus about when needing a stimulus influences its processing without the wanting component for that stimulus, and when ‘Wanting’_{ST} happens without ‘Needing’_{ST}.

As discussed, neuroimaging studies in the activation pattern of ‘Wanting’_{ST} related value shows consistent activation of the striatum, amygdala and insula (Knutson et. al 2003; O’Doherty, 2004; Knutson et. al 2001; O’Doherty et. al, 2002; Wilson et al., 2018; Oldham et. al., 2018; Carter et, al., 2009; Schott et. al., 2008). Those same regions have also been found in the activation pattern of ‘Needing’_{ST} (van der Lan et al., 2011; Goldstone, et. al., 2009; Siep et. al., 2009; LaBar et. al., 2011; Führer, 2008; Mohanty, 2008). It’s not clear how these regions contribute to either ‘Wanting’_{ST} or ‘Needing’_{ST}. Our goal is thus to use a meta-analytic approach to compare the consistent brain activation patterns for ‘Wanting’_{ST} and ‘Needing’_{ST} related values by identifying similarities and differences between the brain activation patterns of these two states that guide value attribution and our consumption behaviors. To do this, we will quantitatively identify the consistent activation patterns after the observation of a reward cue/reward prediction (‘Wanting’_{ST}), versus while (or after) observing a food cue when hungry (‘Needing’_{ST}). We will then directly compare these activation patterns by conducting meta-analytic conjunction and contrast analyses.

METHODOLOGY

We decided to use a meta-analytic approach as it provides an opportunity to quantitatively assess brain activation patterns of ‘Wanting’_{ST} vs. ‘Needing’_{ST} related values using large collections of data. This is useful as a summary of the existing literature is needed, not just because both concepts have rarely been directly compared and are often studied separately in neuroimaging studies, but also because each study might have low replicability, analytical and experimental flexibility, and/or small samples. Thus, our approach aims at identifying and comparing regions that are consistently activated for ‘Wanting’_{ST} and those that are consistently activated for ‘Needing’_{ST}. Specifically, we first conducted two meta-analyses to quantitatively summarize results from functional magnetic resonance imaging (fMRI) published studies on the reward prediction for ‘Wanting’_{ST} (activation maps taken when participants received a reward predicting cue that triggers reward seeking); and on perceiving food stimulus while being hungry for ‘Needing’_{ST} (activation maps taken when participants perceived food while hungry). Second, we did a conjunction analysis to identify common regions that are consistently activated in both

states. Finally, we contrasted ‘Wanting’_{ST} and ‘Needing’_{ST} consistent activation patterns by testing, [‘Wanting’_{ST}-‘Needing’_{ST}], and [‘Needing’_{ST}-‘Wanting’_{ST}].

Included articles

Based on the view that ‘Wanting’_{ST} rests upon reward prediction that has been turned into a decision (see Berridge & Aldridge, 2009) we used the following keywords to identify articles related to ‘Wanting’_{ST}:

((“prediction” AND “anticipation”) OR “desire” OR “wanting”)

Based on the view that ‘Needing’_{ST} such as hunger depends on interoception (Craig, 2003) coming from deprivation of something biologically important, we used the following keywords to identify articles related to ‘Needing’_{ST}:

(“alliesthesia” OR “interoceptive” OR “loss aversion” OR “need” OR “homeostasis” OR “modulating factor” OR “self-specificity” OR “self-referential” OR “hunger” OR “food deprivation”).

While the previous lists of keywords were specific to either ‘Wanting’_{ST} or ‘Needing’_{ST}, the following keywords were the same for both ‘Wanting’_{ST} and ‘Needing’_{ST}; those keywords were the following:

(“reward” OR “motivation” OR “goal directed” OR “decision-making” OR “seeking” OR “incentive”) AND (“fMRI”)

These include words that are often conceptualized as related to ‘Wanting’_{ST} and to ‘Needing’_{ST} (Bouton, 2016; Panksepp, 2004).

For both ‘Wanting’_{ST} or ‘Needing’_{ST}, the following inclusion criteria were used: healthy subjects; whole-brain analyses (with or without SVC), MNI or Talairach Coordinates (all Talairach coordinates were converted to MNI SPM152 in Ginger ALE using Lancaster transform); maps were corrected (or cluster level corrected); activation contrast only.

With regard to ‘Wanting’_{ST}, we typed the keywords on PubMed (February 2021). The database returned 159 articles. The main selection criteria were the presence of a cue that predicts a reward and triggers reward seeking contrasted with no prediction of reward (reward prediction > no reward prediction). After evaluation based on these criteria, 19 final articles were selected out of 26 that were fully read ; and from which we found three additional articles from reviews and other articles that met all the criteria for ‘Wanting’_{ST} for a total of 22 selected articles (see table 2 for list of retained articles). Note that these rewards were mostly money or points, so they are not (directly) related to food, but they are used because ‘Wanting’_{ST} or incentive motivation activates a general system, regardless of the type of stimulus (Bindra, 1968; Bouton, 2016). See Prisma in supplementary material for step by step exclusion of articles.

Regarding ‘Needing’_{ST} related articles, we typed the keywords on PubMed (February 2021). The database returned 376 articles. The main logic was to select experiments when subjects were in a hungry state and perceiving a food stimulus. We looked for both “hunger > baseline” as well as “hunger > satiety” contrasts, because of the inherent subtraction logic of fMRI and in order to have a larger number of experiments. Hence, the two main criteria were : 1) presence of a privation contrast: hunger +stimulus > satiety +stimulus, or hunger+stimulus > baseline; 2) the participant was perceiving some food stimulus which could be presented in any modality : visual, taste, odor, etc. Using the selection criteria (see table 1 for all criteria) we kept 26 articles. After fully reading the final 26 articles, nine were selected, and we found some additional ones through other articles and reviews, and seven among them matched all criteria for ‘Needing’_{ST} (hunger) for a total of 16 articles (see table 3 for list of retained articles). See Prisma and supplementary material for step by step exclusion of articles.

In order to more easily disentangle ‘Wanting’_{ST} vs ‘Needing’_{ST}, the experiments included in ‘Wanting’_{ST} did not include need states, and the ‘Needing’_{ST} related experiments did not include situations in which a cue triggers behavior/reward seeking. This might be viewed as nonfasting vs fasting, but such interpretation should be taken cautiously as it's not about the same reward type and ‘Wanting’_{ST} and ‘Needing’_{ST} are dependent on different situations/paradigms and reward cue roles. Of note, ‘Wanting’_{ST} studies did not explicitly exclude food related studies and were not limited to secondary rewards. However, our selection criteria resulted in the fact that we did not find food related ‘Wanting’_{ST} studies to include. Hence, unintentionally, ‘Needing’_{ST} included primary reward whereas ‘Wanting’_{ST} included secondary rewards and motor action. For ‘Needing’_{ST}, the included studies used a contrast on perception of food related stimuli while hungry vs while satiated. Thus, brain activity elicited by food itself would cancel out, and only the ‘Needing’_{ST} part should remain. Regarding the experimental task, we share the view that ‘Wanting’_{ST} is related to the preparatory and motivational excitement for motor behavior, specifically within the NAcc (Cardinal et al., 2002). Aside from that, the ‘Wanting’_{ST} contrast is between anticipation of a reward cue vs anticipation of non reward cues, where participants responded whether they were rewarded or not. In that sense, motor preparation per se would likely cancel out or would not account for all the brain regions of such contrast.

Meta-analyses

Meta-analyses were conducted with the activation likelihood estimation (ALE) approach using the Brainmap's GingerALE application. Independently introduced by Turkeltaub and his colleagues (2002) and by Chein and colleagues (2002) and revised by Eickhoff and colleagues (2009), the ALE meta-analysis treats activation foci not as single point, but as spatial probability distributions that are centered at the given coordinates (Eickhoff et. al, 2012). The Eickhoff and colleagues's revised ALE algorithm (2009) models the spatial uncertainty by using an estimation of the inter-subject and inter-laboratory variability (which is typically observed in neuroimaging experiments). Then, union of activation probabilities for each voxel of all included experiment is computed to give an ALE map; and a permutation procedure (in which data sets are created similar to the real data in terms of number of experiments, foci per experiments and number of subjects, but in which foci are randomly distributed) is used in order to test the differentiation

between true convergence of foci and random clustering (Eickhoff, et. al, 2012). As a method of inference, the new algorithm uses random-effects analysis that calculates the above-chance clustering between experiments. Furthermore, the new algorithm gives more weight to grey matter compared to white matter by limiting the meta-analysis to an anatomically constrained space specified by a grey matter mask. Contrasts analyses are based on two different datasets (i.e. two previous ALE results) and thus compare two different sets of foci for statistically significant differences; and the conjunction is the intersection of the thresholded maps.

In our analyses we used the MNI152 coordinate system and the less conservative (larger) mask size. For ‘Wanting’_{ST}, there were 21 articles, 34 experiments, 3306 subjects and 572 foci. (See table 2 and 3 for all included articles.). For ‘Needing’_{ST} (hunger), we had 16 articles, 38 experiments, 733 subjects and 494 foci. In our study, for main individual meta-analyses, all maps were thresholded using a cluster-level family-wise error (cFWE) correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ (uncorrected at the voxel level) (Eklund et al., 2016; Woo et al., 2014), and 1000 permutations. For the contrast meta-analyses we used the two cFWE corrected maps with $p < 0.01$ (uncorrected at the voxel level), 10,000 permutations (see Eickhoff et. al., 2011); and the conjunction was the intersection of the two cFWE thresholded maps. Maps from meta-analyses were overlaid on a MNI template and viewed using Mango (<http://ric.uthscsa.edu/mango/>).

Our inclusion criteria (such as including only corrected results and experiments) lowered the number of included experiments. Thus, to confirm that our main meta-analytic results were not driven by the coordinates from a single publication, we conducted validation analyses using a leave-one-experiment-out (LOEO) approach. In this approach, on each fold, one contrast (i.e., experiment) was excluded and the ALE meta-analysis was conducted on the remaining $N - 1$ contrasts. Thus, results from this procedure consisted of brain regions that were identified in every fold of the LOEO, and are not mainly driven by a single contrast.

RESULTS

Main meta-analyses

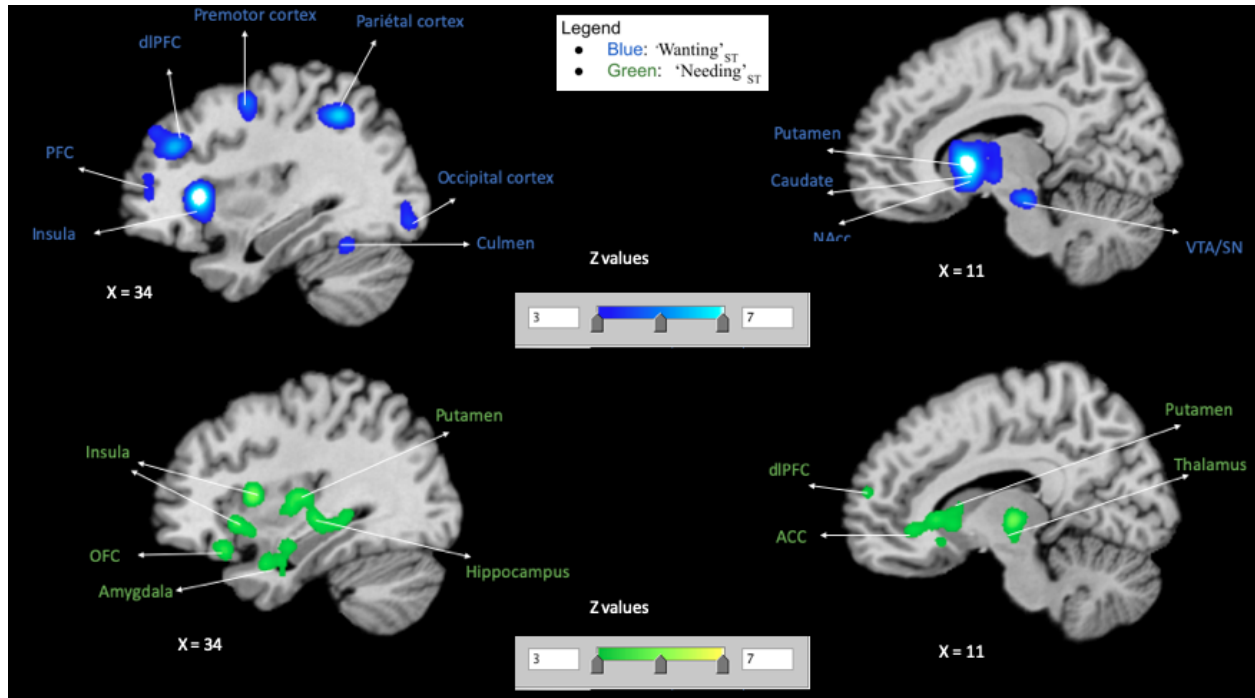
‘Wanting’_{ST}

Our first meta-analysis was on ‘Wanting’_{ST} (*table 4 and figure 1*). This meta-analysis revealed consistent activations within the following regions: the left putamen, the left globus pallidus (which encompassed the nucleus accumbens), the left caudate body and right caudate head, the left substantia nigra, the right red nucleus (encompassing the ventral tegmental area), the right hypothalamus, the bilateral thalamus, the left precentral gyrus, the left inferior parietal lobule, the right dorso-lateral and medial prefrontal cortex, the right superior parietal lobule, the right claustrum (whose cluster was mainly the anterior insula). Of note, because we had much more MID (monetary incentive delay) tasks (see Kutson et al., 2000) in the ‘Wanting’_{ST} contrast, we conducted a single meta-analysis with only studies that did not use the MID task (please see non-MID task meta-analysis in the supplementary material), and we found peak activity within the ventral and dorsal striatum, the dopaminergic midbrain (VTA/SN) and anterior insula. Thus, though experimental tasks for ‘Wanting’_{ST} included a lot of MID tasks, other included paradigms elicited (separately from the MID tasks) the same mesolimbic dopamine and ventral striatal network that has been related to incentive salience ‘Wanting’_{ST}, although in terms of overall whole brain pattern they might have differed.

‘Needing’_{ST}

Next, we conducted an individual meta-analysis on Needing’_{ST} (hunger with stimulus; *Table 5 and figure 1*). This second meta-analysis revealed consistent activations in : the bilateral anterior insula, right middle and posterior insula, right thalamus, left claustrum, right hippocampus, bilateral putamen, right caudate body, right caudate head (encompassing the NAcc), and right posterior putamen (encompassing the caudate tail), amygdala, bilateral anterior cingulate area (encompassing the right OFC), right uncus and left subcallosal area (which can be considered as entorhinal cortex (Fischl et al., 2009), and the right mammillary body.

Figure 7



Single meta-analyses maps

Maps for activated clusters in each condition: 'Wanting'_{ST} (blue) and 'Needing'_{ST} (green), showing activation pattern for each.

Validation Results (LOEO Analyses)

The key output from the LOEO analysis was related to the robustness per cluster. That is, in what probability percentage a given cluster was observed. Here, we show from the LOEO analysis brain regions that have 100% probability of being activated in all experiments included in the meta-analyses.

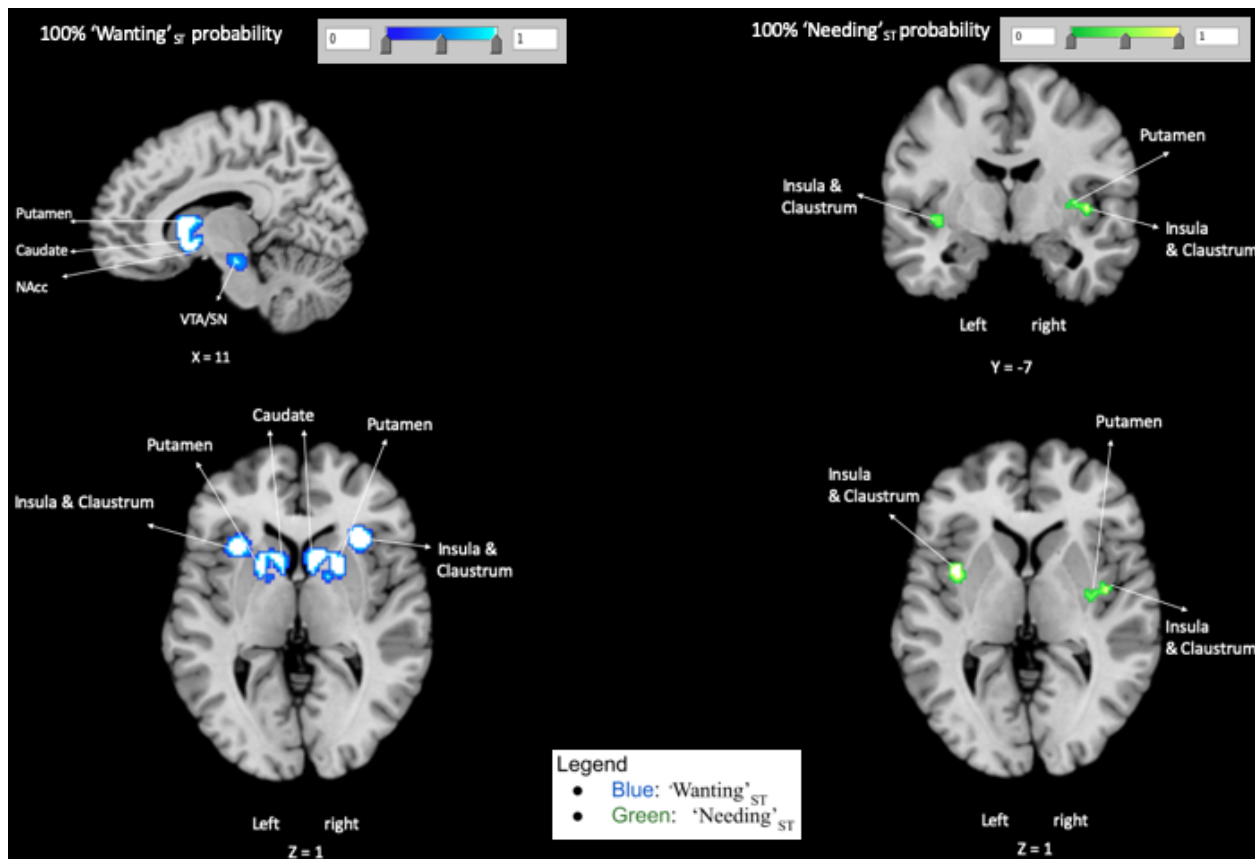
“Wanting”_{ST} (supplementary material and figure 2)

For ‘Wanting’_{ST}, consistent activations were identified in ALE-LOEO with 100% probability in the following peak regions: right midbrain (VTA and SN), right putamen (that included the caudate and the NAcc), left ACC, left caudate, left OFC, left anterior insula, left Inferior Parietal Lobule.

‘Needing’_{ST} (supplementary material and figure 2)

Regarding, ‘Needing’_{ST} ALE-LOEO meta-analysis revealed 3 peaks with 100% consistent activations in all experiments, within the bilateral middle insula, that included the caudoventral putamen and the claustrum.

Figure 8.



100% probability maps

LOEO Maps for clusters of 'Wanting'_{ST} (blue) activation pattern and 'Needing'_{ST} (green) activation pattern that have 100% probability of being activated in each included experiments.

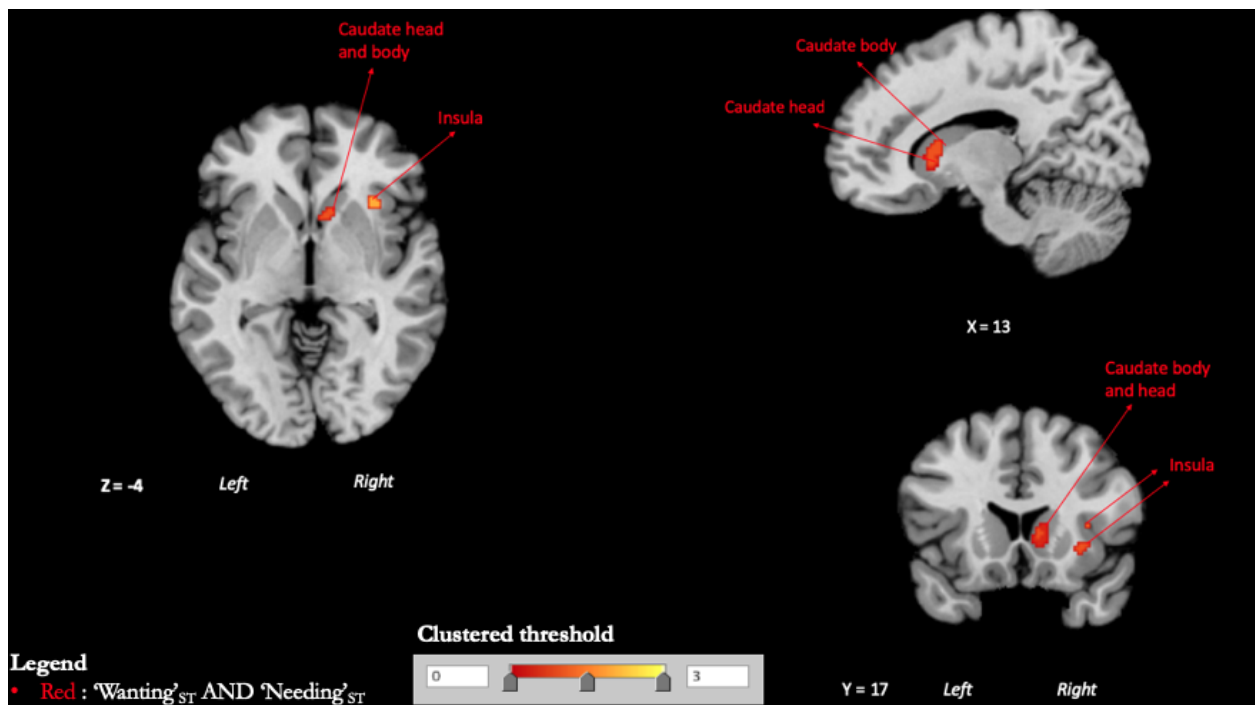
Conjunction and contrasts meta-analyses

Contrasts and conjunction analyses were based on ALE results of the two previous ALE results ('Wanting'_{ST} AND 'Needing'_{ST}) that were compared for statistically significant differences and similarities.

'Wanting'_{ST} AND 'Needing'_{ST} conjunction

The conjunction between ‘Wanting’_{ST} AND ‘Needing’_{ST} resulted in consistent activations within the head and body of the right caudate nucleus (the activated region does not include the nucleus accumbens), right claustrum and right anterior insula (*Table 6 and figure 3*).

Figure 9.



Conjunction maps

Clustered thresholded maps showing the intersection between activation patterns of 'Wanting'_{ST} and 'Needing'_{ST}.

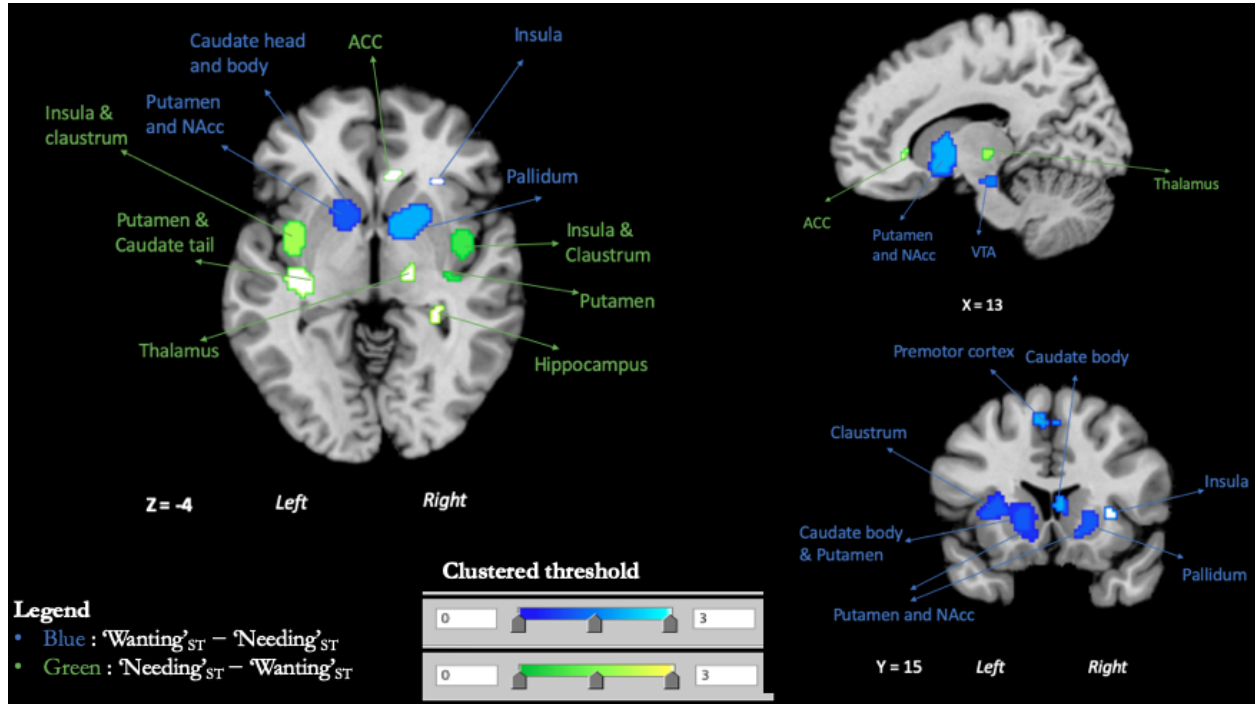
Contrast: 'Wanting'_{ST} - 'Needing'_{ST}

Compared to 'Needing'_{ST}, 'Wanting'_{ST} more consistently activated regions of the left lateral globus pallidus (which encompassed the nucleus accumbens), the left red nucleus (encompassing the ventral tegmental area), right substantia nigra (SN), bilateral putamen, left anterior insula, the left precentral gyrus, the right superior parietal lobule, the left inferior parietal lobule, the right claustrum, the left anterior dorsolateral prefrontal cortex, and the right angular gyrus (*Table 7 and figure 4*).

Contrast : 'Needing'_{ST}- 'Wanting'_{ST}

Compared to 'Wanting'_{ST}, 'Needing'_{ST} more consistently activated regions of the right mid-posterior insula, bilateral claustrum, left putamen (encompassing the tail of caudate), right anterior cingulate area, right thalamus and bilateral hippocampus (*Table 8 and figure 4*).

Figure 10.



Contrasts maps

In blue, clustered thresholded maps for clusters of subtraction $\{['Wanting'_{ST}] \text{ minus } ['Needing'_{ST}]\}$. In green, clustered thresholded maps for clusters of subtraction $\{['Needing'_{ST}] \text{ minus } ['Wanting'_{ST}]\}$.

DISCUSSION

Our goal was to compare the brain activation patterns related to value that comes from the state of 'Wanting'_{ST} from the one from the state of 'Needing'_{ST}. Our study was thus about when needing a stimulus influences its processing without the wanting component for that stimulus, and when 'Wanting'_{ST} happens without 'Needing'_{ST}. To answer this, we used an ALE neuroimaging meta-analysis, comparing consistent brain activation patterns during processing of stimuli in these two states. We used the perception of a cue predicting a reward for 'Wanting'_{ST}; and we used the perception of food stimuli in a hungry state as a model for 'Needing'_{ST}. We first

carried out separate meta-analyses on Wanting'_{ST} and on 'Needing'_{ST}, then we contrasted and intersected them to identify differences and similarities between each of these states. We show that processing a stimulus in a 'Wanting'_{ST} state seems more related to activity within the mesolimbic dopaminergic brain areas, nigrostriatal dopaminergic regions, and striatal regions; while processing a stimulus in a 'Needing'_{ST} state seems more related to activity in viscerosensory cortices (e.g. mid-posterior insula) and caudal-ventral putamen (and to some extent the caudate tail). Both states seemed to share consistent activation in the caudate nucleus (head and body) and anterior insula. Compared to 'Needing'_{ST}, 'Wanting'_{ST} more consistently activated the mesolimbic dopamine: the VTA and ventral striatum and pallidum, and nigrostriatal dopamine regions (i.e. SN and dorsal striatum). Compared to 'Wanting'_{ST}, 'Needing'_{ST} more consistently activated the mid-posterior insula and ACC, caudo-ventral putamen and Caudate tail, and hippocampus. In the following paragraphs, we will discuss our overall results (the ones consistently found in all our meta-analyses) and how by identifying the brain areas most implicated for each state ('Wanting'_{ST} vs 'Needing'_{ST}) can help us understand how we attribute different types of value to stimuli.

Overview of consistent activation patterns for Wanting vs. Needing

Overall, our results--from main individual meta-analyses, LOEO analyses, and contrasts--confirm that the activation pattern of 'Wanting'_{ST} related value shows consistent activation of VTA, ventral striatum, putamen, pallidum and anterior insula. Our results are in line with previous human studies using a wide range of methods or approaches (O'Doherty et. al, 2002; O'Doherty, 2004; Krebs et. al., 2009; Carter et, al., 2009; Schott et. al., 2008; Oldham et. al., 2018; Knutson et. al 2003; Knutson et. al 2001; Wilson et al., 2018; Simon et. al., 2015). For 'Needing'_{ST}, our results-show that only the middle insula and to some extent the caudal-ventral putamen are consistently related to 'Needing'_{ST} related value. The implication of the insula and dorsal striatum in 'Needing'_{ST} is in accordance with some previous literature findings (Goldstone, et. al., 2009; van der Laan, et. al., 2011; Siep et. al., 2009). However, previous meta-analyses and studies on 'Needing'_s had also identified other regions such as OFC, ACC and amygdala/parahippocampal gyrus (Führer et. al., 2008; LaBar et. al., 2011; Mohanty, et. al.,

2008; Chen & Zeffiro, 2020). This could be due to the fact that we report here, regions that have been consistently found in all our meta-analyses (main, contrasts, and LOEO) and thus use a more stringent approach than in previous meta-analyses. Indeed, when only looking at results from our main meta-analysis, we also identified regions within the OFC, ACC and the amygdala. Nevertheless, using a more stringent approach, our results showing consistent activation mainly restricted to the mid-posterior insula make sense as it is often considered as the core viscerosensory cortex because it projects to other visceromotor cortices (anterior insula, OFC, ACC) (Barrett & Simmon, 2015); and dense multimodal sensory interoceptive prediction errors converge within the posterior insula to guide interoception (Gerlach et al., 2020). Thus, by combining contrasts, individual and LOEO meta-analyses approaches, we were able to show that the core regions for ‘Needing’_{ST} (in this case hunger) seems to be the mid-posterior insula).

‘Wanting’_{ST} is more of an emotion than Needing’_{ST}

Our conjunction results showing consistent activations within the anterior insula for both ‘Wanting’_{ST} and ‘Needing’_{ST} could be related to the fact that this region integrates emotional states and is associated with emotional representation of internal states (Craig, 2010), and increases the significance of external stimuli that are relevant with regard to bodily, affective and sensory information (Young & Nusslock, 2016; Menon and Uddin, 2010). Moreover, based on the fact that the anterior insula plays an important role in awareness (Craig, 2011), our findings suggest that this common activation could be related to our ability to be aware of our wants and needs. It is important to note that the anterior insula was found in the contrast ‘Wanting’_{ST} - ‘Needing’_{ST}, but not in ‘Needing’_{ST} - ‘Wanting’_{ST}. ‘Wanting’_{ST}, viewed as reward seeking is often considered as an emotional state (Panksepp, 2004) that may recruit the anterior insula during reward anticipation without necessity of ‘Needing’_{ST} (Knutson et. al, 2001; see Craig, 2010). Thus, ‘Wanting’_{ST} can be thought of as a form of emotional reaction triggered by a Pavlovian cue that predicts a reward. Whereas ‘Needing’_{ST} (physiological in this case) is usually considered an homeostatic emotion or sometimes a simple sensation, because physiological needs such as hunger do not seem to meet the criteria to be classified as emotions (see Panksepp, 2004), even though they can be seen as homeostatic emotions (Craig, 2003). In light of this, we speculate that, in humans, ‘Wanting’_{ST} can have more emotional power than ‘Needing’_{ST} because

of the more consistent recruitment of the anterior insula. Though the anterior insula might contribute to turning ‘Wanting’_{ST} into a more conscious desire/craving (Naqvi et al., 2014; Garavn, 2010), ‘Wanting’_{ST} can also influence behaviour without explicit awareness (Berridge and Robinson, 2003; Strack and Deutsch, 2004; Wei et al., 2017).

Short- term value for ‘Wanting’_{ST} vs long- term value for ‘Needing’_{ST}

While consistent activations were found for both states within the striatum, each seems to recruit a different sub-region with the the ventral and rostral parts, i.e. NAcc, ventromedial caudate and rostroventral putamen more consistently found for ‘Wanting’_{ST} and the caudo-ventral part of the putamen (that often included the tail of the caudate) more consistently found for ‘Needing’_{ST}. This spatial difference could be related to the functional roles of these sub-regions including the coding of short vs. long term values of stimuli. Indeed, our results for ‘Wanting’_{ST} are in line with findings that suggest that ventral striatum is more responsive to reward or its prediction than the dorsal striatum (Schultz et al., 2000) and that rostral striatum, mainly the caudate head, encodes short term or flexible value (Kim and Hikosaka, 2015). This is also in line with the view of ‘Wanting’_{ST} as a moment to moment modulation of a cue that predicts reward in synergy with dopaminergic states (Zhang et al., 2009). In contrast, ‘Needing’_{ST}, was more associated with consistent activation within the caudo-ventral putamen (called “putamen tail”, see Kunimatsu et al., 2019) and (to a lesser extent) the caudate tail, both referred to as striatum tail (Amita et al., 2018), regions that acquire long-term values of stimuli based on the historical experience of reward, but not on prediction of rewards (Kunimatsu, et. al., 2019). Thus, in line with theories and previous studies (Kim and Hikosaka, 2013, Zhang et al., 2009; Amita et al., 2018; Kunimatsu et al., 2019), our results might be interpreted as showing that value representation of a wanted vs. needed stimuli rely on distinct regions of the striatum and that this difference could be driven by the temporal aspects or requirement of value processing for each state.

Directional and activational effect of value

The value assigned to stimuli can have a directional effect or activational effect. The directional effect is linked to choice (preference or action selection) and directs towards or away from stimuli, while the activational effect is related to action initiation, maintenance, and vigor (see Salamone et al., 2018). ‘Wanting’_{ST} AND ‘Needing’_{ST} meta-analytic conjunction showed that both states consistently activate the caudate nucleus (head and body) and anterior insula (discussed above), regions implicated in action selection (Hollon et al., 2014; Ito and Doya, 2015; Petzschner et al., 2021) and emotional representation of internal states (Craig, 2010). The caudate is involved in goal directed behavior (Balleine and O’Doherty, 2010; Knutson & Cooper, 2005), and in the pairing between an action and the value of its consequence (Schwabe & Wolf, 2010), such as on the current state of the organism (see Balleine, 1992). Thus, the caudate is implicated in choice/action selection related value (Hollon et al., 2014; Ito and Doya, 2015), and is involved in directional value (Salamone et al. 2016). The implication of the caudate in ‘Wanting’_{ST} AND ‘Needing’_{ST} conjunction suggests both states can influence choice/action selection, i.e., directional value of stimuli. Thus, by doing a meta-analytic conjunction of ‘Wanting’_{ST} AND ‘Needing’_{ST}, we were able to show that both ‘Wanting’_{ST} and ‘Needing’_{ST} can influence the directional value of stimuli. However, as we will see, each state seems to rely on distinct neural substrates to compute this directional value.

Directional value for ‘Wanting’_{ST} seems to arise from activity within the dopaminergic system. The VTA and SN, which contain the main dopaminergic neurons were shown to be more consistently activated for ‘Wanting’_{ST} than ‘Needing’_{ST}. Our results also show that the regions of the ventral striatum, i.e. the NAcc and the ventromedial caudate and rostromedial putamen (Haber & Knutson, 2010) were more consistently activated for ‘Wanting’_{ST} - ‘Needing’_{ST}; as well as the globus pallidus and the ventral pallidum (VP) (not shown). Indeed, incentive salience ‘Wanting’_{ST} is generated when a reward cue is synergistically mixed with the state of mesocorticolimbic circuits (which mainly implicates the VTA, NAcc and pallidum) (Warlow & Berridge, 2021; Zhang et al. 2009). Based on our results, we suggest that the directional value of ‘Wanting’_{ST} towards stimuli comes from the cortico-striato-midbrain pathway, and first starts with the VTA which computes the prediction error that signals change in expected reward prediction (Schultz et al., 1997) and project mesolimbic dopamine to the ventral striatum (NAcc and VP) (Haber & Knutson, 2010). Second, the activity of the NAcc shell which corresponds to

ventrolateral putamen in humans is the final path to the directional value of ‘Wanting’_{ST} (Holmes et al., 2010); and it is known that mesolimbic dopamine activation within the NAcc or ventral striatum has strong influence on the dorsal striatum (Tricomi et al., 2009).

As mentioned before, with regard to ‘Needing’_{ST}, (the reaction to a needed stimulus); the middle insula, which was found as peak in all of our analyses including our contrasts in favour of ‘Needing’_{ST}, seems to be the core regions for ‘Needing’_{ST} (or in this case hunger: when one perceives food while hungry). In this sense, our results confirm that within the insula, it is the middle insula that pairs internal states to relevant external stimuli as argued by Craig (2010). Moreover, our findings dovetail those in the literature that show that the insula plays a role in an “as – if” representation of the bodily state (Damasio, 1994; Naqvi & Bechara, 2010), and that the insula encodes the incentive value of outcomes as a form of incentive memory (Balleine and Dickinson, 2000). Indeed, when hungry or thirsty, the mid-posterior insula simulates future satiety state in the presence of food or water cues for both humans and animals (Chen et al., 2016; Livneh et al., 2020)). Those cues create an interoceptive 'prediction error' (see Barrett Simmon, 2015). Based on interoceptive prediction error from mid-posterior insula, the visceromotor cortices (ACC, OFC, anterior insula) make predictions about desired internal states (Barrett and Simmon, 2015), and enhance the value of stimuli and actions that fulfill the predictions (Petzschner et al., 2021). Based on our results, we suggest that the mid-posterior insula prediction error might be the origin of the directional value of ‘Needing’_{ST} in the same logic the VTA does for ‘Wanting’_{ST}, i.e. by computing a sort of prediction error that influences cue selection (see Arsenaut et al., 2014); and in this case (i.e. for ‘Needing’_{ST}) it’s an interoceptive prediction error (Barrett and Simmon, 2015). In this regard, the directional value of ‘Wanting’_{ST} and that of ‘Needing’_{ST} depend on two different prediction errors: for ‘Wanting’_{ST} the prediction error is computed within the VTA, and for ‘Needing’_{ST} the (interoceptive) prediction error is computed within the mid-posterior insula. Importantly, although we focussed our meta-analysis on the hunger state and the processing of food stimuli, we think that our results can be generalized to other types of needing states and stimuli. Indeed, it is known that the mid-posterior insula receives multimodal sensory interoceptive signals to compute a prediction error (Gerlach et al., 2019).

If both states can give rise to directional/action selection value (albeit differently), only ‘Wanting’_{ST} seems associated to activational value. Indeed, consistent activations within the NAcc was only found in our ‘Wanting’_{ST} meta-analysis, ‘Wanting’_{ST} - ‘Needing’_{ST} meta-analytic contrast, and even when stringent LOEO analyses were used. ‘Wanting’_{ST} has more (compared to ‘Needing’_{ST}) control on activational value because the prediction error signal is sent to the NAcc which (makes those predictions and) has strong influence to the pallidum which has a lot of impact on invigoration of motor action possibly through a more direct connection to the thalamus (Balleine & O’Doherty, 2010; Haber & Knutson, 2010). In line with literature, our results point out that the activational aspects of cue induced ‘Wanting’_{ST} is likely mediated by the mesolimbic dopamine that implicates activation within the central NAcc (see Holmes, 2010; Salamone et al., 2016; Salamone et al., 2018; Salamone et al., 1997; Salamone and Correa, 2002) or ventral striatal regions in general (Haber & Knutson, 2010) which have strong influence on the dorsal striatum (Tricomi et al., 2009). Our results that ‘Needing’_{ST} did not consistently activate dopaminergic regions, are in line with the now admitted fact that needs by themselves don’t have activational value (see Salamone et al., 2018) and are not the main source of motivated behaviour (Bindra, 1974; Berridge, 2004), although they can amplify it (Toates, 1994). The fact that ‘Needing’_{ST} has only the directional part (choice/preference or action selection), not the activational one, means that a needed stimulus must still become ‘wanted’, by altering mesolimbic dopamine reactivity and encountering a relevant reward predicting cue (Zhang et al., 2009), in order to have full motivational value (Bindra, 1974; Toates, 1994; Berridge, 2004). Thus, motivation is better explained by incentive salience ‘Wanting’_{ST} than by ‘Needing’_{ST} (Bindra, 1974; Berridge, 2004). Nevertheless, ‘Needing’_{ST}, can affect ‘liking’ (see Berridge, 2009) (whether for hunger and food or thirst and water) (Dayan & Balleine, 2002; Balleine 1992), and can create expectation of ‘liking’ through "cognitive desire" (see Berridge, 2012) towards a needed stimulus. This latter is more goal-oriented, and based on declarative memories and on cognitive expectations of act-outcome relations (Berridge, 2012). Thus, ‘Needing’_{ST} generates cognitive desire, but not necessarily ‘Wanting’_{ST} (incentive salience) (Berridge, 2012).

One can wonder, if ‘Needing’_{ST} does not provide activational value to stimuli, what motivates exploratory behavior in the hungry state? We think that such exploratory behavior, in absence of any reward cue, is related to what has been called the “seeking system” by Panksepp (2004).

This system is composed of the hypothalamus, the ventral striatum and the VTA (Panksepp, 2004), and can include the ventromedial prefrontal cortex (Panksepp and Biven, 2012; Di Domenico & Ryan, 2017), and is responsible for energized exploratory and search behaviors and investigation, and it does not need to be stimulated by a positive incentive cue (Panksepp, 2004; Harmon-Jones et al., 2013). However, when there is a reward cue, activity of that system contributes to adding incentive salience or ‘Wanting’_{ST} to that cue (Berridge, 2004) and thus turn the exploratory behavior into need-induced ‘Wanting’_{ST} (see Anselme, 2015). Moreover, it should also be noted that need states can direct and somehow elicit behavior even in absence of the energizing effect of incentive salience ‘Wanting’_{ST} (Niv et al., 2006; Balleine, 2005; Salamone et al., 2018), and areas of the ventromedial prefrontal cortex and ACC can elicit goal directed behavior based on internal states, even in absence of a reward cue that prompts and guides the animal (Passingham & Wise, 2012).

Incentive cue (‘Wanting’_{ST}) vs outcome relevant cue (‘Needing’_{ST})

Although ‘Wanting’_{ST} and ‘Needing’_{ST} are constructs that surely extend beyond the kind of reward, the interpretation of the present results should be done with caution as some brain areas might be indeed influenced by the type of reward, namely the difference between primary (food for ‘Needing’_{ST} experiments) and secondary (money or points for ‘Wanting’_{ST} experiments) reward. Of note, ‘Wanting’_{ST} studies did not explicitly exclude food related studies and were not limited to secondary rewards, but our selection criteria resulted in the fact that we did not find food related ‘Wanting’_{ST} studies to include. However, we believe that, in our study, the difference is not in terms of the kind of reward, but in terms of situations or paradigmes, as was also argued by Sescousse et al. (2013) who conducted a meta-analysis between primary and secondary reward, and found higher dopaminergic striatal activation for secondary reward. They argued that it “is unlikely to be related to the very nature of monetary rewards”, but more about the “protocols used” (Sescousse et al., 2013). In other words, it is unlikely that there is more dopaminergic activation within the ventral striatum for monetary (secondary) reward compared to food or sex (primary) reward, and the difference is indeed in the paradigm (situation) used rather than the type of reward (Sescousse et al., 2013). In our view, the cues in the ‘Wanting’_{ST} experiments were incentive stimuli, i.e. stimuli that motivate action and bias behavior (see

Robinson et al., 2014); whereas the reward cues included in the ‘Needing’_{ST} experiments were not, though they were relevant for the current (deprivational) state (see Balleine, 2005). Thus, though the type of reward can influence some brain activation, it's the role (rather than nature) of the reward cue, based on paradigms or situation, that mainly differentiate between ‘Wanting’_{ST} and ‘Needing’_{ST}, and generate either mesolimbic related reward prediction/prediction error or interoceptive prediction/prediction error, respectively. In a similar paradigm (i.e. where a food cue triggers action to gain it), hunger and/or food (used here for ‘Needing’_{ST}) would also activate ‘Wanting’_{ST}, and would result in dopamine related ventral striatum activation (Simon et al., 2015, 2016; Yousuf et al., 2018). Of note, ‘Wanting’_{ST} studies did not explicitly exclude food related studies and were not limited to secondary rewards. In ‘Wanting’_{ST} experiments that include food, food cues elicited higher mesolimbic dopaminergic response in the ventral striatum when participants were hungry, and such activity was reduced for food cues when participants were satiated (Yousuf et al., 2018). This can be viewed as hunger elevating mesolimbic dopamine, which peaked at the event of the food cue as argued in incentive salience theory (Berridge, 2004; Berridge, 1996). Thus, ‘Wanting’_{ST} is closely related to the presence of a cue, associated to either primary or secondary reward, that triggers action or approach behavior based on mesolimbic dopamine state, and that can happen with or without need state (see DiFeliceantonio & Berridge, 2012). Though we found no study in which participants are in need of money, it is possible that passively viewing money pictures would not necessarily lead to significant mesolimbic dopamine activity, i.e. ‘Wanting’_{ST}, if those pictures are not cues to pursue monetary rewards. Also, it's not sure whether, if one needs money, passively viewing money cues would trigger activity in the mid-posterior insula in the same way as food/hunger or water/thirst (Livneh et al., 2020). Both these hypotheses would need to be empirically tested. In brief, ‘Wanting’_{ST} and ‘Needing’_{ST}, provide two different roles/values to reward cues, depending on situations or paradigms. ‘Wanting’_{ST} related cues are stimuli that motivate action and bias behavior (see Robinson et al., 2014); whereas the ‘Needing’_{ST} related cues are stimuli that are outcome-relevant for the current need state (see Balleine, 2005); and those two roles/values don't necessarily (or always) go together. In that sense, our findings and discussion are more about a difference between such cue roles/values, rather than a difference between primary and secondary reward

Implication on addiction and other maladaptive behaviors

The conceptualization of ‘Needing’_{ST}, when it happens without ‘Wanting’_{ST} somehow dovetails recent neurobehavioral theories of addiction (including food addiction, but see Gearhardt et al., 2011) (for a review see Bickel et al., 2018). Our study, showing VTA and ventral striatum for ‘Wanting’_{ST}, mid-posterior insula for ‘Needing’_{ST}, and anterior insula for both, allow us to speculate that there might be at least two sources of origin of addiction-like behavior. One would be related to interoception, likely gated by the insula, with the mid-posterior insula receiving aversive states information (Livneh et al., 2020; Gehrlach et al., 2020) as found in our ‘Needing’_{ST} - ‘Wanting’_{ST} contrast ; and anterior insula turning such information into emotion, desire and craving (Craig, 2009; Noel et al., 2013; Turel & Bechara, 2016) as shown in our ‘Wanting’_{ST} - ‘Needing’_{ST} contrast and conjunction map. Whereas the other source of addictive behavior would be related to dopamine activity, mainly in the striatum (Hogarth et al., 2013; Volkow et al., 1999; Robinson & Berridge, 1993; Berridge & Robinson, 2016) as found in our ‘Wanting’_{ST} - ‘Needing’_{ST} contrast. This could lead to difference between “addiction” and “dependence” (see O'Brien et al., 2006), with addiction being related to excessive consumption, and thus more related to ‘Wanting’_{ST}. Whereas dependence would be more related to aversive states caused by withdrawal symptoms (that can happen in absence of addiction., see O'Brien et al., 2006), and thus more closer to ‘Needing’_{ST}. The difference could also be temporal; with the beginning of addiction and establishment of sensitization related to striatal dopaminergic areas, thus ‘Wanting’_{ST}; and withdrawal symptoms due to aversives states related to perception of aversive internal states and urge to terminate them within the insula, which includes ‘Needing’_{ST}. Moreover, dopamine related sensitization theory often separates “liking” from “wanting”, where the latter is more responsible for addictive behavior (Berridge & Robinson, 2016). It might be possible to add ‘Needing’_{ST} as a separate component. In that case ‘liking’_{ST} can serve as the beginning of the addictive process, but soon then sensitization happens and is mediated by dopamine related areas and ‘Wanting’_{ST}; and withdrawal is mediated by insula and ‘Needing’_{ST}.

Limits

We would like to point out some limits to our work. First, ‘Wanting’_{ST} experiments did not include physiologically related stimuli such as food or water, We argue that the experiments for ‘Wanting’_{ST} really expressed ‘wanting’ (see Berridge, 2004) because the contrasts we used focussed on the processing of the cues, not the outcome; and the cues in those experiments triggered the decision for reward seeking. Indeed, ‘wanting’ has been related to decision utility, i.e. the “choice to pursue or consume an outcome” (Berridge & O’Doherty, 2014), induced by a cue (Berridge & Aldridge, 2009). So, although we could not know the mesolimbic state of participants in those experiments, the behavioral situations, i.e. a cue that triggered a decision to seek reward, do seem to induce ‘wanting’ (see Berridge, 2004). Furthermore, ‘Wanting’_{ST} or motivation activates a general system, regardless of the type of stimulus (Bouton, 2016). Thus, though most stimuli for ‘Wanting’_{ST} were money or points, the mechanism for cue induced decision for reward seeking, i.e. ‘Wanting’_{ST} is the same.

Second, ‘Needing’_{ST} contrasts only focused on hunger and the processing of food (physiologically related stimuli). Though our method could seem dependent on the type of physiological state, i.e. hunger, and thus the type of needed stimuli, i.e. food; our findings and interpretation seem to go in the same direction than studies and theories that suggest an integrative role of all physiological states within the insula. In that sense Gerlach et al. (2020) results suggest that dense multimodal sensory prediction errors converge in the posterior insula to guide interoception. Based on that, it has been argued that that the insula represents physiological state in cue-independent spontaneous activity, which is then modified directionally by cues that predict water or food availability (Namboodiri & Stuber, 2020). This suggests that our findings regarding the activation of mid-posterior insula might not be hunger/food dependent but rather be resulting from a more general role of the insula with regard to bodily states, specifically serving interoceptive inference (Allen, 2020). Though, there are justifications for our methodology in general, it would still be interesting for future studies to test the difference between ‘Wanting’_{ST} and ‘Needing’_{ST} with more control on the dopaminergic state, on the type of physiological states and on the type of stimuli.

Nevertheless, wanting and/or needing go way beyond eating, drinking or winning money or points. The distinction between wanting vs needing can apply to virtually any decision, and can

even be viewed as philosophical or phenomenological concepts. In that sense, they go way beyond our study and the tools we have used. Thus, our study should be viewed as testing some manifestation of wanting and/or needing rather than testing the general phenomena.

Conclusion

Our goal was to compare the brain representation of ‘Wanting’_{ST} and ‘Needing’_{ST} related values --two states that guide value attribution and our consumption behaviors. Our results suggest distinct brain systems for both states, with the mesolimbic dopaminergic circuitry as the core for ‘Wanting’_{ST} and the posterior-middle insula for ‘Needing’_{ST}. Whereas ‘Needing’_{ST} only provides directional value (through an interoceptive prediction error), ‘Wanting’_{ST} which involves dopamine provides both directional (through a reward prediction error) and activational value. Because ‘Needing’_{ST} does not provide activational value to stimuli, full motivation (directional and activational) to consume depends more on ‘Wanting’_{ST} than on ‘Needing’_{ST}, and means that ‘Wanting’_{ST} has more power to activate behavior. This might explain why we consume what we want beyond what we need (Stearns, 2006).

AUTHOR CONTRIBUTION

Juvenal Bosulu: Designed the study, performed the database search, performed data analysis, interpretation, and wrote the manuscript. **Sébastien Héту:** Designed the study, revised the manuscript and provided critical feedbacks. **Max-Antoine Allaire:** Performed the database search, revised the manuscript and provided critical feedbacks. **Laurence Tremblay-Grenier:** Performed the database search, revised the manuscript and provided critical feedbacks. **Yi Luo:** Revised the manuscript and provided critical feedbacks. **Simon Eichkoff:** Revised the manuscript and provided critical feedbacks. All authors contributed to and approved the final manuscript version.

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RÉSUMÉS DE L'ÉTUDE 3

Nos actions et nos choix semblent parfois guidés par nos besoins, parfois par nos désirs et parfois par les deux. La raison pour laquelle il y a parfois association et parfois dissociation entre le besoin et le désir reste largement inconnue. Le besoin est lié à la privation de quelque chose d'important sur le plan biologique, et le désir est lié à la prédiction de la récompense et à la dopamine et possède généralement plus de pouvoir sur l'activation comportementale que les états de besoin seuls. L'étude 3 vise à clarifier leurs relations en utilisant l'inférence active et la théorie de l'information. Dans cette approche, le besoin est lié à une déviation par rapport aux états préférés que les êtres vivants ont tendance à occuper afin de réduire leur surprise, tandis que le désir, c'est-à-dire la prédiction de la récompense, est lié à la précision par rapport à la police menant aux récompenses. À travers une série de simulations, nous démontrons l'interaction entre les systèmes de besoin et de désir. Plus précisément, nos simulations montrent que lorsque les états de besoin augmentent, la tendance à occuper des états préférés est renforcée indépendamment du désir (ou de la prédiction de la récompense), montrant une dissociation entre

le besoin et le désir. De plus, les simulations montrent que lorsque les états de besoin augmentent, la valeur des indices (cues) qui signalent la réalisation de la récompense et la précision des polices qui conduisent aux états préférés augmentent, ce qui suggère que le besoin peut amplifier la valeur d'une récompense et son désir. Pris ensemble, notre modèle et nos simulations aident à clarifier l'influence directionnelle et sous-jacente des états de besoin séparément de la prédiction de la récompense, c'est-à-dire le désir, et montrent en même temps comment cette même influence sous-jacente du besoin amplifie le désir, c'est-à-dire augmente la précision des signaux de récompense qui conduisent à l'état préféré.

CONTRIBUTION DES AUTEURS

Juvéna1 Bosulu : a conçu l'étude, réalisé l'expérience/simulation, analysé et interprété les données, et rédigé le manuscrit. **Giovanni Pezzulo** : a révisé le manuscrit et fourni des commentaires critiques. **Sébastien Hé1u** : a révisé le manuscrit et fourni des commentaires critiques. Tous les auteurs ont contribué à la version finale du manuscrit et l'ont approuvée.

ÉTUDE 3 : A COMPUTATIONAL ACCOUNT OF NEEDING AND WANTING

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ABSTRACT

Our actions and choices sometimes seem driven by our needs, sometimes by our wants and sometimes by both. Why sometimes there is association and sometimes dissociation between needing and wanting remains largely unknown. Needing is related to deprivation of something biologically significant, and wanting is linked to reward prediction and dopamine and usually has more power on behavioral activation than need states alone. This paper aims to clarify their relations using active inference. In this approach needing is related to a deviation from preferred states that living things tend to occupy in order to reduce their surprise, while wanting, i.e. reward prediction, is related to precision over policy leading to rewards. Through a series of simulations, we demonstrate the interplay between needing and wanting systems. Specifically, our simulations show that when need states increase, the tendency to occupy preferred states is enhanced independently of wanting (or reward prediction), showing a dissociation between needing and wanting. Furthermore, the simulations show that when need states increase, the value of cues that signal reward achievement and the precision of the policies that lead to preferred states increase, suggesting that need can amplify the value of a reward and its wanting. Taken together, our model and simulations help clarifying the directional and underlying influence of need states separately from reward prediction, i.e. wanting, and at the same time show how this same underlying influence of need amplifies wanting, i.e. increases the precision of reward cues that lead to the preferred state.

FULL TEXT

1. Introduction

There has been a debate around the question of if people, for instance consumers, are driven by their needs or their wants (Campbell, 1998). “Needing” is related to a state of deprivation of something important for life or survival (Bouton, 2016), and increases arousal through interoceptive salience (Craig, 2003); and not responding to a need might lead to some adverse consequences such as physiological or psychological suffering which go beyond mere frustration (MacGregor 1960; Baumeister & Leary, 1995). “Wanting” is more related to goal achievement and reward prediction and is more closely related to dopaminergic activity and motivation (Berridge, 2004). Both have some influence, albeit differently, on the motivational value of

stimuli. Importantly, motivation can have a directional effect and/or activational effect. The directional effect is linked to choice (preference or action selection) and directs towards or away from stimuli, while the activational effect is related to action and its initiation, maintenance, and vigor or effort (Salamone et al., 2018). Notably, wanting is able influence both activational and directional values of stimuli even in absence of need states: nonhuman animals tend to respond and “want” food even when satiated (Bouton, 2016), and for humans, cues of M&M or pictures of cigarettes (for smokers) have been shown to lead to more consumption even after having been consumed to satiety (Hogarth & Chase, 2011; Watson et al., 2014). On the other hand, needing seems to control directional motivation, but seems to rely on wanting for the activational part ((Dickinson & Balleine 1994; Balleine, 1992; Berridge, 2004; Berridge, 2018; Wassum et al., 2011; Salamone et al., 2018).

At the brain level, needing and wanting systems could map to partially different neural substrates. A recent fMRI meta-analysis compared consistent brain activations during needing (perception of needed stimuli, i.e. food when hungry) and during wanting (perception of a reward cue that leads to reward seeking). It showed that needing seems more related to brain regions implicated in directional motivation/value; whereas wanting seems to be more related to brain regions implicated in both directional and activational motivation/value, and to mesolimbic dopaminergic areas (Bosulu et al., 2022). Furthermore, these results suggest that needing is related to interoceptive predictions and prediction errors as well as cues related to interoceptive states, such as food cues, possibly computed within the mid-posterior insula (Bosulu, et al., 2022; Livneh et al., 2020), while wanting is instead related to exteroceptive (e.g., cue- or reward-related) predictions and prediction errors, with the latter possibly computed within the ventral tegmental area (VTA) (Schultz et al., 1997; Bosulu, et al., 2022). Hence, needing seems to be more related to the internal environment, whereas wanting seems to be more related to the external environment, although this is not necessarily a strict separation as – for example – wanting could also take into account the internal environment (Berridge, 2004).

However, needing and wanting systems are not segregated but might influence each other reciprocally. Biological needs, such as those related to states of deprivation of a biologically

significant stimuli or events (Bouton, 2016), seem to influence the rewarding aspect of biologically relevant stimuli, such as wanting, pleasure and choice. For instance, food is often more wanted, liked and chosen when hungry. Thus, although it has been shown that motivation to pursue rewards depends more on expectations (e.g., reward prediction), than on needs states (Bindra, 1974; Berridge, 2004), need states tend to amplify reward predicting cues that are relevant to such need states (Toates, 1994; Berridge, 2004). Need states can also enhance liking of, and pleasure related to, relevant stimuli that satisfy one's needs (Cabanac, 2017; Berridge & Kringelbach, 2015; Becker et al., 2019). Moreover, a need state has the capacity to give and to control the preference/choice or value of a novel food or drink or of a particular choice or action, in relation to their consequence on the organism (Dickinson & Balleine 1994; Balleine, 1992), and such need related action happens via a system that could be both dependent (Berridge, 2004; Berridge, 2018) and independent of dopamine (Wassum et al., 2011 Salamone et al., 2018). Furthermore, in absence of a reward guiding cue, a need state can (directly) activate relevant actions (Passingham & Wise, 2012) or explorative behavior (Panksepp, 2004). Overall, this indicates that biological need states are able to influence certain tendencies towards relevant needed stimuli, hence affecting wanting and goal directed choices (and liking).

To sum up, our previous discussion illustrates that needing and wanting systems could link to different aspects of motivation (i.e., directional and activational) and to partially different neural substrates and states (i.e., internal and external) – but at the same time, they might interact in various ways. Yet, we still lack a comprehensive computational framework that accounts for the findings reported above and that specifically explains (1) how could internal needs exert a directional influence on goal-directed behavior and choice, even in absence of wanting and (2) how could a state of needing amplify wanting (and liking).

The main goal of this paper is to provide a computationally-guided perspective on needing and wanting, which helps make sense of the fragmented literature on these topics. In the following sections, we will firstly address the two above questions conceptually, using formal methods from active inference, information theory and reinforcement learning (Parr et al., 2022; Sutton and Barto, 2018). Then, we present two simulations that address the functioning of needing and wanting systems – and their interactions – more formally.

2. Needing and wanting systems and their interactions: a conceptual perspective

2.1 The directional influence of needs on goal-directed behavior and choice

The goal of organisms is to regulate internal states and keep them within certain very limited boundaries (Barrett, 2017; Sterling & Laughlin, 2015; Friston, 2006). For instance, the average normal body temperature for humans is generally between 36.1°C (97°F) to 37.2°C (99°F), which is a very small range compared to the range of possible temperatures in the universe, from the absolute zero to trillions of degrees. The same is true for levels of glucose or the balance between water and salt in the body. The main idea is that the number of "states" that make life possible are really small compared to the very large number of other combinations that wouldn't sustain life. So, to allow a living organism to remain within its normal physiological boundaries, natural evolution might have set them as so-called (empirical) priors, which might be conceived as (possibly genetically encoded) innate preferred states that the organism always strives to achieve. These preferred states (corresponding to physiological bound) have a greater probability to be reached from the point of view of the organism, i.e. are less surprising (Friston, 2010). Here, the surprise associated with a state, denoted $h(y)$, is the inverse of being probable and simply means less probable. Anecdotally, for a fish, being out of water would count as a surprising state. Any self-organizing system must minimize such surprise in order to resist a natural tendency to disorder (Friston, et al., 2006; Friston, 2010) and in the case of our fish, death.

Formally, the notion of surprise is closely related to the notion of entropy. Entropy, denoted as H , is the long-term average of the surprise and (here) it expresses the uncertainty related to which state must be occupied. If an organism is endowed with a prior about the states to occupy (i.e., with one or more preferred states), achieving these high probability states reduces surprise and its long-term average: entropy (Parr et al., 2022; Friston, 2010). By the same token, higher probability translates into more preference: living creatures naturally prefer the most probable states that sustain life. Thus, distancing from those states leads (or equivalently, being in a surprising state) entails an (informational) cost that living beings strive to minimize.

Importantly, the notion of being in a surprising state (or in other words, being far from preferred states) links well to the concept of "needing" discussed in the Introduction. In the same way

being in a surprising state entails an (informational) cost, a state of need entails a (biological) cost if a person does not respond to the need (see MacGregor 1960; Baumeister & Leary, 1995). When a living organism moves away from its preferred state, it is in a state of "need" - which amounts to having a tendency to occupy preferred states (again). The state of need can be represented as:

$$h_n(y) = - \ln P(y|C) \quad \text{Eq. 1;}$$

where h_n represents the “need-related” surprise of a sensation or state y , which is equal to the negative log probability of being in (or observing) a state y given the distribution of prior preferences, denoted as C . Note that for simplicity, in this article we will collapse the notions of “state” and of “observation that can be obtained in the state”, which are typically distinct in active inference (and more broadly, in Partially Observable Markov Decision Processes); see the simulations below.

The perception of a need state translates into a “goal” of reducing surprise by reaching the preferred states, e.g., states that represent adaptive physiological conditions (Friston, 2010). Such tendency could activate an action or a policy (i.e., an action pattern or sequence of actions) that compel creatures to seek out the (valuable) preferred states. Note that the actions or policies that resolve a state of need could in some cases correspond to (fixed) regulatory actions, such as autonomic reflexes, as opposed to action courses determined by the circumstances of the external environment (Sajid et al., 2021). The states that the creature occupies when pursuing a policy that resolves a need can become valued per se (Friston & Ao, 2012). In other words, when the creature pursues a course of actions towards the preferred state, all the intermediate states (here intended in a broad sense that encompasses situations, actions, stimuli, etc.) can become valued and needed. For instance, when moving from a state of hunger to a state of satiety, some intermediary states could be the gustatory stimulus associated to having food and the act of eating; and such states would become valued, because they are in the path towards the preferred (satiety) state (Pezzulo et al. 2015). Through this mechanism, a creature would experience the need for food or the need to eat – and then start to prefer the valued states, stimuli or actions. In other words, the directional effect of need states on motivation could come from the tendency to occupy preferred states.

In turn, as noted above, pursuing preferred states reduces “need related entropy” and the surprise associated with occupying non-preferred states. In this sense, the tendency to occupy preferred states confers to need states the possibility to influence – and give value to – stimuli or actions that are either costly states $S(h_n)$ that lead to surprise, or in the path towards the preferred state $\pi(p)$. In other words, in an environment where there are increasingly costly/surprising states, any state (stimulus or action) that is in the path to the preferred state will become valued (needed) because it reduces entropy.

2.2 How needing amplifies wanting

The effect of needing on wanting (and on other phenomena such as pleasure and liking) could be conceptualized by appealing to the formal notion of precision in active inference. Mathematically, precision is a term used to express the inverse of the variance of a distribution which in our context can be seen (loosely speaking) as the inverse of entropy (Friston, 2010; Holmes 2022) – in the sense that the higher the entropy, the lower the precision. In predictive coding and active inference, precision acts as a multiplicative weight on prediction errors: prediction errors that are considered more precise have a greater impact on neural computations (Parr et al., 2022).

In active inference, there are different precisions associated with different forms of changes in prediction, such as interoceptive, reward or policy predictions (see Parr et al., 2022). Of particular relevance here is the precisions of policies, which indexes the confidence that we have that by following a particular policy we will reach a preferred (goal or reward) state. Crucially, while we pursue a policy, every cue or information that confirms (reduces uncertainty about the fact) that a policy will achieve a preferred state enhances policy precision. This is the case for example if we are following a route that we hope will lead to a given city (or to a restaurant that we hope is open) and we encounter a traffic sign that indicates that the direction to the city is correct (or a sign that the restaurant is open).

At the neurophysiological level, policy precision, or the confidence that a policy will lead to reward, is typically associated with the dopaminergic system in active inference (FitzGerald et al., 2015; Parr et al. 2022, Holmes, 2022). Therefore, reward cues that enhance our policy

precision and our confidence that the policy will lead to reward would trigger dopamine bursts, which will attribute incentive salience to such cues (Berridge, 2007). This is in line with the idea that dopamine is linked with incentive salience and wanting; but also with reward prediction and behavioral activation as they typically co-occur (Hamid et al., 2016). Rather, precisions regarding hedonic contact with the reward (to ask questions such as: is it good?) or the state of satiety (to ask questions such as: am I well?) might be mediated by the opioid system (Berridge & Kringelbach, 2015) and the serotonin system (Parr et al., 2022; Liu et al., 2020; Luo et al., 2016), respectively.

Interestingly, these systems are interdependent. When one is in a surprising (need) state, the presence of a cue (e.g., a traffic or restaurant sign) might reduce our uncertainty about goal/reward achievement by improving policy precision via dopamine system activity (wanting); the presence of, or contact with, the reward itself might reduce entropy by enhancing precision through the opioid system (pleasure/liking); while being directly in a preferred state or towards the preferred state could be related to precision via serotonin (well-being). All of these contexts serve as information that reduce entropy by signaling the availability of a path to preferred states ($\pi(p)$), or equivalently away from surprising states (h_n), given some prior preference.

The policies discussed so far depend on exteroceptive cues from the environment. As discussed above, these cues (e.g., cues that signal a reward) can become imbued with incentive salience and "wanting" (Berridge, 2007) in virtue of the fact that they enhance policy precision. The increased policy precision that comes from the presence of rewards (or of cues that signal incoming rewards) means more certainty that the state to which the policy leads will be rewarding, and it is this certainty that amplifies wanting. This mechanism could function relatively independent from a state of need. For instance a relatively satiated animal that smells some food, will be motivated to follow the smell because doing this increases the probability of finding food. However, its wanting (and the associated dopamine firing) could be amplified if the animal is in a need state. If the animal that smells food is hungry, it will be motivated to follow the smell, not just because there is a high probability to secure food, but also because that food will be very rewarding. That is, the animal will be more certain (i.e., have greater precision) that it should pursue a policy that leads to the predicted reward. It's in that sense that needing amplifies wanting. It is also possible to speculate that the hungry animal will likely have more

pleasure while eating food than the satiated one – because it could assign more certainty (precision) to how good food is when it is hungry.

To summarize, we propose that the wanting mechanism is intrinsically related to the fact that cues afford some resolution of uncertainty (e.g., about what policy to pursue) and linked to the dopaminergic system. Indeed, “wanting” depends on external stimuli that act as pavlovian cues that predict rewards (Berridge, 2018), and the attribution of value to these cues depends on mesolimbic dopamine reactivity which can be enhanced by physiological states (needs, emotions, drugs, etc.) (Berridge, 1996; Berridge, 2004). Furthermore, we propose that the influence of needing on wanting can be conceptualized as a need-induced enhancement of the precision of policies and thus of the saliency of the rewards, stimuli or actions that lead to the preferred state.

2.3 Summary

Our discussion so far has highlighted two important points about needing and wanting systems, and their interactions. First, need states exert a directional influence on choices separately from wanting (and reward prediction). In the perspective offered here, need states gain their underlying (motivational and saliency) effect from the tendency to occupy preferred states. When a living system moves away from such preferred states towards “costly” states, a state of need is generated. Being in costly or need states automatically increases the probability of activating policies that lead to preferred states. Hence, the mere state of deprivation of need has an underlying directional effect and influences the tendency to reach rewarding or goal states. This tendency exists irrespective of reward prediction, as conceptualized for example in model-free reinforcement learning systems, which can be related to wanting (Zhang et al., 2009; Berridge, 2004).

Second, by the same token, the underlying influence of need amplifies wanting, by increasing the value of reward cues that signal the possibility to reach goal states (hence lowering uncertainty about goal achievement) and the precision of goal-achieving policies. The simultaneous circumstance of being in a need (hence surprising) state and encountering a cue that signals that a goal state is achievable (hence that surprise and uncertainty can be reduced) is the ideal condition

to confer goal-achieving policy with a very high precision. By indicating that there is a path to a goal or reward state, the cue renders the organism more confident about what to do - and this is amplified when the gain in reward (or the amount of surprise minimized) is greater, such as when one is in a need state. This is why need states amplify “wanting” by enhancing the value of cues and the precision of policies that lead to preferred goal states.

In the next sections, we move from the conceptual treatment offered in this section to a formal implementation of the proposed model of needing and wanting. Subsequently we illustrate the functioning of the model in two simulations, which illustrate how being in need/costly states influence the tendency to reach rewarding/preferred state (Simulation 1), and how the simultaneous presence of a state of need and the presence of a path to the preferred (reward or goal) state implies low entropy and high precision over which state to occupy (Simulation 2).

3. Methods and Results

3.1 Simulation environment

Our simulations regard a very simple situation, mimicking the idea of agents that have to remain within a limited physiological (e.g., food or temperature) bound. For this, we designed a grid-world environment in which only one state is rewarding/preferred, whereas the number of surprising/costly states is much greater (See Figure 1). We can draw a parallel between the grid-world and human physiological states, such as hunger or temperature: the preferred state corresponds to the optimal interval of sugar level in the bloodstream, or the temperature range (between 36.1°C (97°F) and 37.2°C (99°F)). In the grid-world, each interval of sugar level, or of temperature range, is represented as a specific state in which the agent can be (each state corresponds to a box in Figure 1).

Specifically, we used a 3x3 grid-world containing nine states, eight “costly states” (states 0, 1, 3, 5, 6, 7, 8) and a reward/preferred state (state 2), whose value is initially unknown to the agent. There are two terminal states (not shown) reachable from states 2 and 5, i.e., states that, once occupied, cannot be left by the agent. State 2 represents a reward/preferred state that gives a

reward of 1 and state 5 leads to death (which is as costly as the other states, but from which the agent can never come back).

Figure 11.

<i>state 0</i>	<i>state 1</i>	<i>state 2</i> <u><i>reward</i></u>
<i>state 3</i>	<i>state 4</i>	<i>state 5</i> <u><i>death</i></u>
<i>state 6</i>	<i>state 7</i>	<i>state 8</i>

The environment

Grid world environment used in our simulations. Each box represents one state in which the agent can be. These include eight costly states (states 0, 1, 3, 4, 5, 6, 7, 8) and a reward state (state 2). The value of these states is initially unknown.

In our simulations below, the only thing that we will vary is the amount of cost associated with the eight “costly states”. We will do so by assigning to these eight states the same negative reward (-1, -2, or -5) representing a significant departure from biological bounds. Note that the agents that dwell in the simulated environments do not know these values and will have to compute the *expected* biological costs, or values by themselves (see below for a description of the agents that we will use in our simulations).

3.2 Simulation agents

Our simulations will consider two agents: an active inference agent that embodies our hypotheses about needing and wanting systems and that implements tendencies or prior preferences over policies; and a reinforcement learning agent that computes reward prediction in the form of action values (Parr et al., 2022; Sutton and Barto, 2018). Note that at each time step, the two agents receive an observation about their current state and then they can self-localize in the grid map; and they can move one step vertically or horizontally, but not diagonally.

Agent 1: active inference agent

Agent 1 is a simplified version of active inference, in which the perceptual part is kept as simple as possible, by assuming that all the states of the grid world are observable. Technically, this means that we are dealing with a Markov Decision Process (MDP) and not a Partially Observable Markov Decision Process (POMDP) as more commonly done in active inference (see Friston et al., 2009; Friston et al., 2017). This simplifying assumption is motivated by the fact that our focus in this work is on action selection and not perceptual discrimination. Furthermore, keeping the perceptual part simple facilitates the comparison with the reinforcement learning agent (see Agent 2 below) that uses an MDP, too.

The costs and rewards assigned to states translate directly into a prior preference for these states (denoted below as C), with rewarding states being a-priori more probable than other states. Since the agent expects to occupy (or to move towards) these a-priori probable states, the prior over states also translates into priors over actions or action sequences (policies) that achieve such states. In this simplified setting, action (and policy) selection simply corresponds to inferring a distribution of states that it prefers to occupy and policies to reach (sequences of) these states. In other words, the active inference agent tend to select policies that lead it to achieve goal states - which in Bayesian terms corresponds to maximizing model evidence.

More formally, under the simplifying assumptions discussed above, the active inference agent strives to maximize a measure of (log) evidence, defined as:

$$\ln [P(y)] \quad \text{Eq. 2}$$

where \ln denotes a natural logarithm and $(P(y))$ the probability of observing a state (remind that in our setting, hidden states and observations are the same; hence $y = s$.) Equivalently, active inference agents strive to minimize surprise, defined as the negative of the evidence:

$$-\ln [P(y)] \quad \text{Eq. 3}$$

Importantly, as remarked above, for active inference agents what is surprising or not surprising depends on prior preferences (e.g., a fish out of water is in a “surprising” state). In this perspective, being in a surprising state (i.e., far from prior preferences) is what defines a state of “need”. To account for needs, we condition the surprise to priors C (prior preferences, i.e. biological costs or rewards) and we get a need-related surprise:

$$-\ln [P(y|C)] \quad \text{Eq. 4}$$

This equation represents the surprise or negative “value” of an observation/state, given the organism’s prior preferences. In turn, the prior preferences play a role in prioritizing policies, which correspond to courses of actions that try to reduce current and future (expected) surprise. When one accounts for policies (π), the expected surprise given the prior preferences is:

$$- E_{Q(y|\pi)} \ln [P(y|C)] \quad \text{Eq. 5}$$

The $E_{Q(y|\pi)}$ part means that the probability of states/outcomes is averaged across all policies (π).

In active inference, the quantity shown in Eq. 5 $E_{Q(y|\pi)} \ln [P(y|C)]$ (without the minus sign) is typically called a “pragmatic value” and in this setting, it corresponds to the expected free energy $G(\pi)$ (an upper bound on expected surprise):

$$G(\pi) = - E_{Q(y|\pi)} \ln [P(y|C)] \quad \text{Eq. 6}$$

For completeness, it is important to consider that the quantity shown in Eq. 6 (without the minus sign –the ”pragmatic value”–is only one of the two terms of the expected free energy $G(\pi)$ of active inference ; however, in our setting, the second term (“epistemic value”) is zero, and hence here we simply ignore it.

The expected free energy $G(\pi)$ is particularly important since it is used for policy selection. Specifically, active inference agents are equipped with a prior over policies, denoted as $P(\pi)$. The greater the expected free energy that policies are expected to minimize in the future, the greater their prior, i.e.,

$$P(\pi) = \sigma(-G) \quad \text{Eq. 7}$$

where σ represents the softmax function, bounded between 0 and 1, and enforces normalization (i.e. ensures that the probability over policies sums to one).

This $P(\pi)$ is what will be used as prior over policies by the agent 1 in order to select policies (which, in our simple scenario, reduce simply to actions) and ultimately to minimize surprise.

Agent 2: model-free reinforcement learning

The second agent makes decisions based on prediction of rewards assessed by state-action values, i.e. each decision will depend on the value of actions given the current states (see Sutton & Barto, 2018). Here the policies depend on the action values, denoted $Q^\pi(s, a)$, and given by:

$$Q^\pi(s, a) = E_\pi\{R_t | s_t = s, a_t = a\} = E_\pi\{\sum_{t=0}^{\infty} \gamma^t r_{t+1} | s_t = s, a_t = a\} \quad \text{Eq. 8}$$

The equation shows the value or “quality” (Q) of the action (a) in state (s) under a policy (π). The function denoted $Q^\pi(s, a)$ expresses the expected (E) return (R), which is the (expected) sum of rewards, starting from state (s) and taking the action (a), and thereafter following policy (π). Here the state s for agent 2 is equivalent to the state/observation y of agent 1.

The agent's decision after learning is based on the optimal policy π_* , i.e. the one that maximizes the expected return, and therefore the optimal $Q^\pi(s, a)$, noted $Q^*(s, a)$ is equal to:

$$\max_a Q(s, a) \quad \text{Eq. 9,}$$

where \max_a is related to the action that maximizes $Q(s, a)$.

In sum, the two agents differ in their policy selection mechanism. Agent 1 (active inference) uses a prior over policies $P(\pi)$ illustrated in Eq 7, whereas agent 2 (reinforcement learning) uses action values $Q^*(s, a)$ illustrated in Eq 9 which, here, amounts to reward prediction. The goal of our first simulation, illustrated below, is to assess the effects of increasing need states on the action selection mechanisms of the two agents.

3.3 Simulation 1: Directional aspect of needing separately from reward prediction

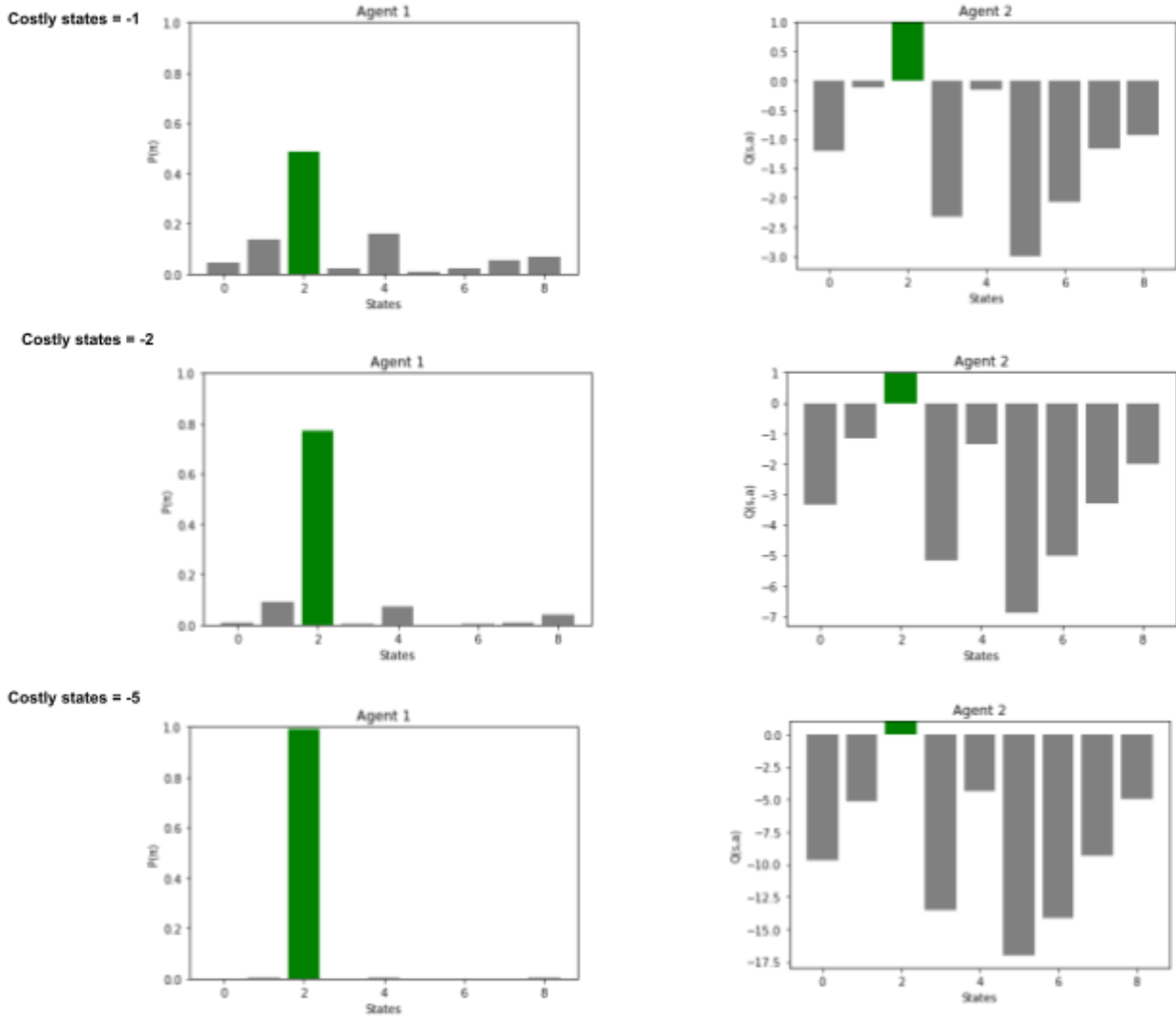
In this simulation, we consider the effects of increasing the costs of the eight “costly states” of Fig. 1 from -1, to -2 and -5 on action selection of active inference (left panels of Fig. 2) and reinforcement learning agents (right panels of Fig. 2), respectively. For this, we calculate for each level of need/cost (i.e. -1, -2, -5) the prior probabilities of policies $P(\pi)$ that reach each of the states of the grid-world (Agent 1) and the state-action values that emerge from reinforcement learning (Agent 2). To calculate the probabilities of policies of Agent 1, we use active inference,

as explained above. Rather, to calculate the action values of Agent 2, we use a standard Q learning approach and let Agent 2 learn by trial and error, by navigating in the grid map (for 1000 trials).

The results illustrated in Fig. 2 show that increasing the costs of the eight “costly states” significantly increases the probability assigned to policies that reach the rewarding state in the active inference agent (Agent 1). This is evident when considering that the probability increases from (about) 0.5, 0.8 and 1 in the three left rows. However, increasing the costs of the eight “costly states” does not affect reward prediction in the reinforcement learning agent (Agent 2). This is evident when considering that the state-action (Q) values assigned by the reinforcement learning agent to the rewarding state is always 1 in the three right rows (this is because the true reward provided by the state is 1).

These results help illustrate the idea that costly or need states might exert directional effects and impact on the probability (or tendency) to reach preferred states, irrespective of reward prediction. In other words, expected biological costs do not control or constrain values directly, but directly control probabilities, i.e. policies or tendencies, to be in (or go to) the preferred states. This directional effect of needs is well captured by active inference agents, which increases the probability to reach rewarding states when “in need”. Conversely, a reinforcement learning approach to estimate the reward guaranteed by the preferred state correctly infers the reward itself but it is not sensitive to the magnitude of the "need" of the organism.

Figure 12.



Simulation 1

Effects of biological needs on policy selection under active inference (Agent 1, left panels) and reinforcement learning (Agent 2, right panels). Note that in the bottom panel of the RL agent, the value of state 2 is 1 as for its other two panels. The left and right panels show the results for active inference (Agent 1) and reinforcement learning (Agent 2), respectively. For active inference agents, the y axis plots priors over policies $P(\pi)$ to reach each of the states of the grid-world, whereas for reinforcement learning agents, the y axis plots state-action (Q) values. The three rows show the effects of setting the costly states (states 0 to 8 except state 2, see Fig. 1)

to -1, -2 and -5, respectively. The results show that increasing biological needs (across the three rows) increases the probability that Agent 1 selects policies to reach the preferred state 2, but does not increase per se the state-action value assigned by Agent 2 to state 2. This is consistent with the idea that need (directionally) influence tendencies (i.e. probabilities) more than reward prediction. See the main text for explanation.

3.4 Simulation 2: How needing amplifies wanting

Simulation 1 showed that action selection in the active inference agent (Agent 1) is sensitive to need states. In Simulation 2, we ask if being in a state of greater need amplifies the wanting of the active inference agent, when a reward is present (note that here we do not consider Agent 2, as the results of Simulation 1 show that it was not sensitive to the magnitude of the "need").

For this, we consider an active inference agent dwelling in an environment in which the costs associated with costly states vary from -1, -2 and -5, which correspond to the fact that the agent faces milder or more severe conditions of "need". We consider (1) the entropy over the states that it plans to occupy in the future by following its inferred policy and (2) the inverse of the above entropy, i.e., the precision, which is a measure of certainty about which states to occupy in the future. We compare two conditions; namely, when there is a reward (i.e. the reward state 2 is baited with a reward of 1) and when there is no reward (i.e., the reward state 2 has the same cost as all the other costly states).

We calculate the “need related entropy” (or simply entropy) as follows:

$$H_n(Y = S(h_n)) \quad \text{Eq. 10,}$$

when there is no reward, and

$$H_{n,p}(Y = S(h_n), \pi(p)) \quad \text{Eq. 11,}$$

when the reward is present and the agent has a potential path towards the preferred state. Here, H denotes the entropy and it can be calculated on two sets of states. When the reward is available, the entropy is over the states occupied by the agent while following a policy $\pi(p)$ that leads to the preferred rewarding state (p). Alternatively, when there is no reward, the entropy is over the states $S(h_n)$, or the states S that lead to surprise h_n given the prior preferences (i.e., the need related surprise of Eq. 1).

$Y = S(h_n)$ means Y is $S(h_n)$, and $Y = S(h_n), \pi(p)$ simply means Y can be $S(h_n)$ or $\pi(p)$

The $\pi(p)$ and $S(h_n)$ represent states in different subsets of prior preferences, with the $\pi(p)$ representing states that are on the path to the preferred state. These can be viewed as rewarding (or cues) states or events that lead (transition) to the preferred state if one follows a policy leading to the preferred state. The $S(h_n)$ represent the states that lead to surprise. This formulation highlights that the (need-related) entropy of an agent that faces costly/surprising states $S(h_n)$ is reduced when there is a path towards the preferred state $\pi(p)$. Thus, the inequality below holds:

$$H \geq H_{n,p} \quad \text{Eq. 12}$$

We calculate the precision as the inverse of the entropy:

$$P_n = H_n^{-1} \quad \text{Eq. 13,}$$

when there is no reward, and

$$P_{n,p} = H_{n,p}^{-1} \quad \text{Eq. 14,}$$

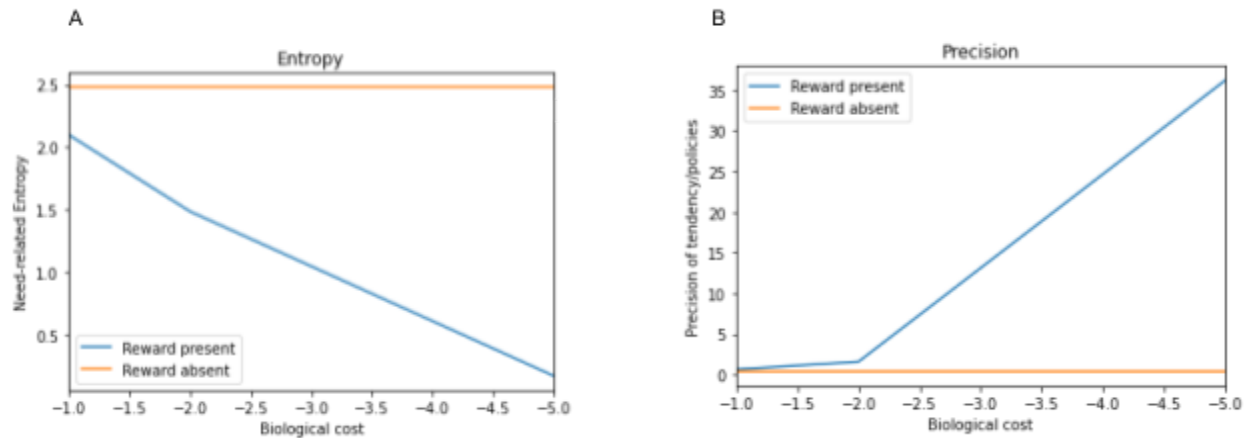
when there is a reward and hence a path to the preferred state / rewarded state. Given the inequality in Eq. 12, when states become more costly, the precision increases, providing that there is a path towards the preferred / rewarded state, which implies that:

$$P_n \leq P_{n,p} \quad \text{Eq. 15}$$

Given that we are discussing the motivational, i.e. active part, here entropy means (average) uncertainty over which state to occupy rather than uncertainty over what state is. Similarly, precision means certainty over what state to occupy. The principle is the same whether applied to what states to occupy or what policy to follow. The idea is to make it general so it can apply to incentive salience (wanting) or to hedonic sensation (liking), and also to simpler organisms that might not have a sophisticated brain.

The results of the simulations of entropy (Eq. 10 and 11) and precision (Eq. 13 and 14) can be appreciated graphically in Fig 3. These results shown indicate that compared to the case with no reward, the condition where a reward is present implies a significant decrease of the entropy over which states the active inference plans to occupy in the path to the reward (Fig. 3, left) and a significant increase of its precision, which is a measure of certainty about which states to occupy in the future (Fig. 3, right). This is because the availability of a reward makes the agent more confident about the states to occupy and the policy to select, whereas in the absence of a reward, all states are equally costly and the agent has no strong preference about which states to occupy (i.e., high entropy and low precision). The presence of a reward (which in this simulation is known by the agent) is a cue that makes it possible to pursue a preferred course of action, reducing the entropy about the states to occupy and increasing the certainty (precision) about the states to visit in the path towards the preferred state (and the precision of the relevant policy, not shown).

Figure 13.



Simulation 2

The impact of different need states on the entropy (left plot) and on its inverse, the precision (right plot), over which state to occupy for an active inference agent, in conditions in which a reward is available (blue lines) or no reward is available (orange lines).

Furthermore, and interestingly, being in a more costly state amplifies the above effects: with greater biological needs and a reward available, entropy reduces and confidence increases. Mathematically, the greater the biological cost of costly (or surprising) states, the lower the probability assigned to them, the higher the probability assigned to the preferred state - and ultimately, the lower the entropy over which state to occupy (as all the probability mass will be on the preferred state). In other words, if the biological cost associated with costly states increases, the agent becomes more confident about where to go and tends to occupy the preferred state with higher probability. In this sense, it is the conjoint presence of costly (surprising, need) states and of preferred (rewarding) states that maximally reduces the agent's entropy over which state to occupy (because the probability of reaching the preferred state increases) and increases its confidence about the path to pursue. To the extent that we associate the above precision (and confidence) with "wanting", these results show that a state of need amplifies the wanting, when there is a reward (or a cue) available.

4. Discussion

"Needing" and "wanting" exert significant influence on our decisions and actions. The former is related to biological costs and the deprivation of something biologically significant, while the latter is more related to reward prediction and dopamine and can usually exert a stronger influence on behavior. However, the respective roles of "needing" and "wanting" systems and the ways they interact are not completely understood. Here, we aimed to provide a computationally-guided analysis of the mechanisms of "needing" and "wanting" and their interactions, from the perspective of active inference theory.

We firstly defined a need state as a "surprising" state in the sense assigned to the term "surprise" by theories like predictive coding and active inference, in which living creatures strive to remain within tight physiological boundaries (i.e. preferred states) and are surprised outside them - like a fish out of water. This perspective suggests that being in a costly or need state may exert a directional effect on action selection and motivation, because creatures would have an automatic tendency to select policies that avoid surprises and lead to preferred states. Importantly, this automatic tendency would be present without any reward or reward cue, which is in keeping with evidence of driving influences of "needing" without "wanting".

Furthermore, we associated "wanting" to the precision of policies that achieve preferred (goal or reward) states, consistent with previous work that linked policy precision to incentive salience and dopaminergic activity (FitzGerald et al 2015, Friston et al., 2017). In this perspective, cues that signal that there is a path to secure a reward are particularly salient and related to the "wanting". Needing and wanting systems are however related, as a state of greater need can amplify wanting: the higher the initial state of need, the greater the wanting of cues related to reward and of reward itself (and possibly also the greater the pleasure of reward consumption).

4.1 Simulation 1. The need system and its directional effect on behavior and motivation

To illustrate these arguments, we performed two simulations in a grid-world with most states associated with costs (to mimic a state of need of the organism) and one state associated with a reward. Simulation 1 illustrates the possible functioning of "needing", by focusing on the action selection mechanisms of two agents: a simplified active inference agent considers the probability

of policies to go to the preferred state and a reinforcement learning agent that considers action values and reward predictions (learned using standard Q learning). This simulation shows that when the active inference agent is in more severe states of needs (i.e., the non-rewarded states of the grid world are associated with a greater cost), it assigns a greater probability to the policies that lead to the rewarding state. Hence, in active inference, a state of need can have a directional influence on behavior, leading the agent towards the preferred states and away from costly or surprising states. Rather, the reinforcement learning agent correctly estimates the reward provided by the rewarding state, but this estimate was not sensitive to the agent's need state. This latter result helps illustrate the idea that the "need" system cannot be reduced to reward prediction per se.

This simulation therefore illustrates nicely the directional and underlying effect of need states: need controls directional motivation, because of the tendency of living beings to move towards preferred states; and such tendency activates policies that lead to the preferred states. In doing so, states within the trajectory of those policies become preferred (and valued). This tendency is mediated by homeostasis or its more general form allostasis (Sterling, 2004; Barrett, 2017; Holmes, 2022; Demekas et al., 2020), which help animals remain within viable physiological boundaries (Sterling, 2004; Holmes, 2022). From the active inference perspective, a living organism continuously strives to reach or remain in its preferred states (which could be sometimes evolutionarily defined, though homeostatic or allostatic regulation, at the somatic, autonomic and neuroendocrine levels (Parr et al., 2022; Swanson, 2000)). These preferred states act as drives or goals that, through homeostasis and allostasis, direct action (Barrett, 2017); hence the directional effect of need states. Such directional influence, dependent on tendency to occupy preferred states, is also responsible for the underlying effect through which need states amplify wanting, pleasure, interoceptive prediction, choice, etc.; by enhancing precision of their related stimuli (or actions) that are in the path towards the preferred state, in an environment of costly/surprising states. This leads to Simulation 2 below.

4.2 Simulation 2: The effects of needing on wanting

Simulation 2 illustrates how the simultaneous presence of state of need and of a reward (and a path to it) can amplify "wanting" in the active inference agent. The simulation shows that the presence (versus the absence) of (a path to) a reward decreases the entropy of the states that the active inference agent plans to occupy and increases the associated precision, or the confidence about occupying these states (and about the policies, not shown in our results). Note that while in this Simulation 2 we focused on a fully observable environment, previous (companion) simulations performed in partially observable environments showed coherent results (Friston et al., 2017). These previous simulations showed that the observation of a contextual cue - namely, of a cue that reveals reward availability and location to the agent - increases the precision of policies and that these precision dynamics can be related to dopaminergic activity. In our Simulation 2, the mechanism is similar (despite the full observability) because the agent is aware that a reward is present and hence there is a path towards the preferred state that realizes the agent's prior preferences. In other words, in both cases, something that signals a viable path to the reward increases the confidence of the agent in its course of actions.

Importantly, our Simulation 2 also shows that the decrease in entropy over which state to occupy, and the increase of associated precision, are magnified when the active inference agent is in a more severe state of need (i.e., when the costs of the non-rewarded states of the grid world are increased) and there is a path to the preferred state. In other words, the more costly (surprising) these states are, the more the agent is certain that it needs to go to the preferred state. This illustrates how need states amplify the wanting (and perhaps also the liking) of stimuli: by reducing entropy and making the agent more confident about what course of action to select. Need states have cascading effects also on the stimuli and actions in the path towards goal or reward states. When in a severe need state, relevant stimuli, reward cues and actions have a greater role in reducing entropy and increasing the confidence in the selected course of actions (Parr et al. 2022, Holmes, 2022). These relevant stimuli, reward cues and actions are therefore assigned a greater value and a greater "need-generated" salience, which neurophysiologically could correspond to increased dopaminergic activity, too.

4.3 Relations between our proposal and previous studies

Our proposal is coherent with previous reinforcement learning models of need's influence on reward value or on incentive salience. A representative example is the "homeostatic reinforcement learning" model of Keramati and Gutkin (2014), according to which any behavioral policy, π , that maximizes the sum of discounted rewards also minimizes the sum of discounted deviations from a setpoint. In other words, the maximization of a needed reward also minimizes the deviation caused by such need (Keramati and Gutkin, 2014). This idea is related to our approach, in that the need state is related to a deviation from a setpoint; however, in keeping with active inference, the setpoint is modeled as a prior and each deviation from it implies a "surprise", as explained above.

Another related approach is the computational model of wanting and incentive salience by Zhang and colleagues (2009). This model introduces a physiological variable, k (representing dopaminergic state), which changes the value of reward, r , in turn resulting in an amplification of the value of states, $V(s)$; specifically, the amplified value is denoted as $\bar{V}(s_t) = \bar{r}(r_t, k) + \gamma V(s_{t+1})$, with γ representing a discount factor, t denotes the time step and $V(s_{t+1})$ denotes the value of the next state. Hence, the value of a reward cue depends on the combination of the reward value r and the dopaminergic states k . If r can be a proxy of reward that assigns state values, and k , is influenced by the need states (e.g., hunger or thirst, etc) then \bar{r} , which is the function of the combination of r and k , reduces entropy. The state value $\bar{V}(s_t)$ can be enhanced by both the physiological need state k (surprising state) and the value of the reward r , that signals the path to the preferred state (p). The amplification of reward is a function of the reward itself and of k , that is: $\bar{r}(r_t, k)$. Here, the reward is (on) the path to the preferred state. Hence, replacing or interpreting the path to the preferred (rewarding) state as $\pi(p)$ and the physiological state k as the need state that lead to surprise $S(h_n)$, we obtain that the function of the enhanced reward \bar{r} , which is encoded as confidence by dopamine, is related to precision over policies leading to reward. This is the inverse of need related entropy, i.e. inverse of the function

$$H_{n,p}(Y = S(h_n), \pi(p)),$$

or in other words the function

$$\bar{r}(r_t, k) = H_{n,p}^{-1} (Y = S(h_n), \pi(p)) = H_{n,p}^{-1} = P_{n,p}$$

This implies that there is a direct correspondence between the model discussed here and Zhang's (2009) model. However, the treatment offered here allows a more general treatment as it expresses needing, wanting and their interactions in terms of information-theoretic quantities, namely, information and uncertainty.

More broadly, a number of studies show that needing and wanting can occur both together and separately (see Bosulu et al., 2022; Berridge, 2004). As our Simulation 1 illustrates, needing (in the sense of a tendency to occupy the preferred states) can occur without wanting (which is more related to reward achievement and prediction) and can influence a preference for courses of action that lead to preferred state, even when such influence is not directly linked to reward prediction (as the results of the reinforcement learning agent show). When needing and wanting for a stimulus (or action) happen together, need states tend to amplify wanting (Berridge, 2004 ; Toates, 1994) by increasing precision, or saliency, of wanted cues - as illustrated in Simulation 2.

Furthermore, although here we are mainly concerned with the precision of future states occupied by the agent, as discussed there are different precisions associated with different forms of changes in prediction (see Parr et al., 2022). So in principle, a state of need could increase different forms of precision, or salience, of stimuli or cues that are on the path to a reward and are typically associated with wanting and "incentive salience" (see Berridge 2004). Furthermore, a state of need could increase the (precision-mediated) liking and pleasure associated with stimuli that are available. For instance, for need states to amplify pleasure, the agent must come into contact with the reward (e.g. have food in the mouth when hungry).

Importantly, a precondition for the amplifying effect of need states on wanting is the presence of a cue that predicts that the course of actions will lead to a reward. Bosulu and colleagues (2022) conducted a fMRI meta-analysis on perception of needed stimuli in absence of wanting (i.e. significant stimuli were shown but the task did not explicitly state that they would be available after) and found that need states did not seem to sufficiently and consistently activate the dopaminergic system, which is related to wanting. This might be due to the fact that the stimuli associated with needing that were used in the studies included in the meta-analysis did not act as

strong cues that the same stimuli would be obtained in the future. It is in this sense that needing can happen independently of wanting. However, the same study showed consistent activity within the mid-posterior insula during the perception of needed stimuli (Bosulu et al., 2022), which might be interpreted as an indication that needing can amplify the precision relative to interoceptive predictions, even in absence of a “true” reward prediction. The same study discusses how wanting, which is more related to reward prediction and can generally happen without needing (Bindra, 1974; Berridge, 2004), can be amplified by internal states other than the need states, such as emotions, stress, drugs, etc. (Berridge, 1996; Berridge, 2004). This likely means that those non-need related internal states can amplify wanting-related precision. Furthermore, need states are perhaps not the only ones to generate entropy or influence the reactivity of the dopaminergic system. The activation of the dopaminergic system in relation to a range of phenomena, such as stress, emotions, etc. can amplify wanting even in absence of need states (Berridge, 1996; Berridge, 2004). The scope of all these interactions between needing, wanting, bodily and emotional processing and dopaminergic activity remains to be fully mapped in future studies.

Our treatment suggests that both states of need and reward cues (related to wanting) influence behavior, but differently. When the agent is in a state of need, there is an automatic tendency to resolve it and then the organism could tend to follow preferred policies or state transitions (which can be at least in part considered to be genetically encoded and related to homeostatic and allostatic mechanisms) irrespective of cues that signal reward availability. Rather, wanting could be more related to reward prediction and its associated policies could be triggered by the availability of reward cues. The above arguments lead to the suggestion that the needing systems could be more related to internal (prior) policies that are more automatic and wanting could be more related to learned and external policies, i.e. changes in the environment related to prediction of reward which can be attained by the behavior, likely related to the somatic motor system (Swanson, 2000). This might be one of the reasons why wanting has more control over behavioral activation (Bosulu et al., 2022; Salamone et al., 2018; Berridge, 2004), but at the same time need can modulate wanting (Berridge, 1996 ; 2004) just as it can modulate liking (Berridge, 2007), preference (Balleine, 1992), etc. - in a way that here we characterize formally as a need-related precision.

Yet, as our Simulation 2 showed, needing and wanting systems can act synergistically. For example, need states increased precision when there is a reward leading to the preferred state. In that sense, if the reward determined by the need states, i.e. by the prior (internal) policy, is the same as the reward predicted by a signal of reward which specifies the external policy, then the precision will be enhanced and needing and wanting will be synchronized.

In sum, this study aimed at providing a conceptual model that defines needing and wanting systems and their interactions; and to demonstrate some of the peculiarities of these systems with the aid of simulations based on the framework of active inference. However, the relations between the relatively abstract notions introduced in this article, such as need-related entropy, and their biological substrates, remain to be fully clarified and tested empirically. A more systematic mapping between the information-theoretical notions used here and neurobiological evidence is an open objective for future research.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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AUTHOR CONTRIBUTION

Juvenal Bosulu: Designed the study, performed the experiment, data analysis, interpretation, and wrote the manuscript. **Giovanni Pezzulo:** revised the manuscript and provided critical

feedback. **Sébastien Héту**: revised the manuscript and provided critical feedback. All authors contributed to and approved the final manuscript version.

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SECTION V : DISCUSSION GÉNÉRALE

Dans cette thèse, nous avons comme objectif principal de comprendre la différence entre besoin et désir, et ce, dans l'optique d'expliquer la concordance (association) et la discordance (dissociation) entre les deux. Dans ce qui suit, les manifestations du besoin et du désir seront discutées, tant dans leurs patrons d'activations cérébrales que dans leurs natures théoriques. Par la suite, la discussion portera sur la manière dont ces manifestations peuvent expliquer la concordance et la discordance entre ces deux états.

MANIFESTATION DANS LE CERVEAU

Il existe un patron d'activation cérébrale commun aux besoins physiologiques et sociaux qui semble corrélé davantage avec le récepteur 5HT4 que les autres récepteurs de la sérotonine

Les résultats de la première étude suggèrent que les régions de l'insula mi-postérieure (portions entre l'insula du milieu et l'insula postérieure), de l'ACC «pregenual» (prélimbique) et du noyau caudé sont des régions où il y a convergence d'activité cérébrale liée à la perception des stimuli physiologiques (pour la faim et la soif) et sociaux (pour l'exclusion) dont nous sommes privés. Ces résultats suggèrent que les besoins physiologiques et les besoins sociaux sont tous deux reliés d'une manière ou d'une autre à l'interception. Ainsi, l'idée d'examiner les zones cérébrales communes entre les stimuli physiologiques et sociaux dont nous sommes privés a permis de montrer que les états de besoin en général pourraient avoir un patron commun d'activation cérébrale. Les résultats montrant le chevauchement entre besoins physiologiques et sociaux, notamment au niveau de l'insula mi-postérieure, suggèrent qu'il est possible de généraliser les résultats de l'étude 2 qui ne portaient que sur les besoins physiologiques (la faim) à d'autres formes de besoins, y compris aux besoins sociaux. De plus, les résultats de l'étude 1 sur la corrélation spatiale entre les régions d'activations constantes et communes aux deux types de besoins et la distribution spatiale des récepteurs de la sérotonine soulignent que, parmi les récepteurs de la sérotonine, le récepteur 5HT4 pourrait avoir un rôle important dans la relation entre ces régions communes et l'activité de la sérotonine. En se basant sur la littérature

concernant ce récepteur, on peut spéculer qu'il permettrait aux états de privation/besoin ou aux stimuli dont on a besoin d'influencer l'activité des neurones de la sérotonine via le réseau commun d'activation trouvé dans la méta-analyse de l'étude 2 (voir Rebholz, et al., 2018 ; Takagishi and Chiba 1991 ; Peyron et al., 1998 ; Lucas et al, 2005 ; voir aussi Price, 2007 ; Weston, 2012 ; Castello, et al 2018 ; Geddes et al.2016).

Quant aux patrons d'activation, on les retrouverait dans l'insula mi-postérieure pour le besoin et le VTA et NAcc pour le désir

L'insula mi-postérieure, qui a été trouvée comme pic dans toutes nos analyses en faveur du besoin, y compris nos contrastes, autant comme commun aux besoins physiologiques et sociaux (étude 1) que dans la comparaison besoin moins désir (étude 2), semble être centrale pour la manifestation du besoin et la perception de stimuli dont on a besoin. Ceci concorde avec une suggestion de Craig (2010) selon laquelle, dans l'insula, c'est l'insula du milieu qui associe les états internes aux stimuli externes pertinents, tandis que c'est l'insula postérieure qui reçoit ces sensations internes. De plus, nos résultats rejoignent ceux de la littérature qui montrent que l'insula joue un rôle majeur dans la représentation et la simulation de l'état interne actuel et futur, et ce, au regard de la présence ou l'absence des stimuli externes pouvant modifier cet état interne (Damasio, 1994 ; Naqvi & Bechara, 2010 ; Chen et al., 2016 ; Livneh et al., 2020). L'activité dans l'insula mi-postérieure pourrait donc être un biomarqueur pour la perception de stimuli dont on a besoin, séparément du désir. Sur la base des résultats de l'étude 2, le désir envers les stimuli dépendrait de l'activité au sein du système de la DA mésolimbique : notamment le VTA qui contient les neurones dopaminergiques et qui signale la prédiction de la récompense (Schultz et al., 1997) et le NAcc qui facilite les actions pour obtenir ces récompenses (Li et Daw, 2011 ; Berridge et Aldridge, 2009 ; Lex et Hauber, 2008 ; Hamid et al., 2016 ; Zhang et al. 2009 ; Balleine et Killcross, 2006). L'activité du VTA et NAcc serait donc un biomarqueur pour la perception de stimuli qui excitent le désir, peu importe que cela soit en lien avec un état de besoin ou non.

Les stimuli de besoin sont prédictifs de changements intéroceptifs alors que ceux du désir sont prédictifs de récompenses, et ces deux rôles sont séparables

L'étude 2 suggère que les motivations directionnelles envers les stimuli du besoin versus ceux du désir dépendent de deux prédictions différentes : pour le besoin, il s'agirait du fait que la présence du stimulus annonce un changement dans la prédiction interoceptive, codée dans l'insula mi-postérieure. Tandis que pour le désir, il s'agirait du fait que le stimulus annonce un changement dans la prédiction de récompense, codée dans le VTA qui projette dans le NAcc, dont la coquille permet d'exciter l'organisme en direction des stimuli qui prédisent la récompense (Holmes et al., 2010). Ainsi, les stimuli liés au besoin, et qui activent l'insula, possédaient un rôle de prédicteur de changements interoceptifs, de par leurs pertinences pour l'état actuel (de privation) (voir Balleine, 2005). Les stimuli liés au désir sont des stimuli incitatifs, c'est-à-dire des stimuli qui motivent l'action et le comportement en prédisant une séquence (policy) qui aboutit à la récompense (voir Robinson et al., 2014). La deuxième étude a montré que ces deux rôles s'appliquent de manière indépendante aux stimuli selon les situations. Donc, dans le cerveau, il existe une réaction aux stimuli dont on a besoin, même en l'absence d'un désir ; et de la même manière, il existe un désir, qui peut se produire indépendamment du besoin.

Le désir a plus d'impact sur l'activation du comportement, mais le besoin a un effet sous-jacent

En outre, l'étude 2 montre que le désir a constamment activé le complexe formé de VTA, NACC et pallidum. Ceci confirme que le désir a plus de contrôle sur l'effet activationnel par l'action de la dopamine mésolimbique dans le NAcc (Holmes, 2010 ; Salamone et al., 2016 ; Salamone et al., 2018 ; Salamone et al., 1997 ; Salamone et Correa, 2002) lequel a une forte influence sur le striatum dorsal (Tricomi et al., 2009) (région impliquée dans la réponse comportementale), et sur le pallidum, lequel a beaucoup d'impact sur la revigoration de l'action motrice grâce à sa connexion directe au thalamus (Balleine & O'Doherty, 2010 ; Haber & Knutson, 2010). Le fait que le besoin n'a pas cet effet activationnel signifie que normalement un stimulus dont on a besoin doit devenir désiré pour activer le comportement (Bindra, 1974 ; Berridge, 2004) ; et dans ce cas le besoin amplifie le désir (Toates, 1994 ; Berridge, 2004 ; Zhang et al., 2009). Il faut cependant se rappeler que le comportement dont il s'agit ici est celui lié à la division somatique

du système moteur, et il est possible que le besoin ait plus de pouvoir activationnel sur les portions autonome et neuroendocrinienne du comportement (voir Swanson, 2000). Cette possibilité reste à tester. Toutefois, dans les circonstances inhabituelles, par exemple en absence complète de dopamine (Wassum et al., 2011 ; Salamone et al., 2018), ou en absence de prédiction de récompense (Passingham & Wise, 2012 ; Panksepp, 2004), un état de besoin très élevé peut activer le comportement ; probablement par l'effet sous-jacent par lequel les besoins influencent le désir (Toates, 1994 ; Berridge, 2004), le plaisir (Cabanac, 2017 ; Berridge & Kringelbach, 2015), la préférence (Dickinson & Balleine 1994 ; Balleine, 1992), et même les attentes ou désirs cognitifs (voir Berridge, 2012), etc.. Cette influence sous-jacente du besoin est discutée ci-bas.

MANIFESTATION AU NIVEAU DE LA NATURE THÉORIQUE

L'effet sous-jacent du besoin est lié à la tendance d'occuper les états préférés, et ce, indépendamment du désir

La première simulation de la troisième étude a montré que la présence des coûts biologiques (états surprenants), c'est-à-dire des états de besoin, influence les tendances (probabilité des policies) positivement vers les états préférés ; même quand cette influence n'est pas présente dans la prédiction de récompense. Cela explique l'effet directionnel des états de besoin, en ce sens que les états sur la trajectoire de la policy menant aux états préférés deviennent des récompenses, c'est-à-dire valorisés, en présence des états coûteux. Ainsi, le besoin contrôle la motivation directionnelle à cause de l'effet sous-jacent qu'est la tendance des êtres vivants à occuper les états préférés. Ces derniers, probablement définis de manière évolutive (Friston, 2010), sont maintenus par une régulation homéostatique ou allostatique via le comportement (Parr et al., 2022), et ce, au niveau somatique, autonome et neuroendocrinien (voir Swanson, 2000). Dans cette perspective, les états préférés agissent comme des pulsions ou des buts qui, par l'homéostasie et l'allostasie, orientent l'action (Barrett, 2017) ; d'où l'effet directionnel du besoin.

Lorsqu'on est dans le besoin, la présence d'un chemin vers l'état préféré réduit l'entropie et augmente la précision

La seconde simulation de l'étude 3 a montré que lorsque les états surprenants (état de besoin) qui créent de l'entropie deviennent de plus en plus coûteux, l'entropie est grandement réduite s'il existe une récompense ou un signal de récompense qui indique un chemin vers l'état préféré. Comme la dopamine qui cause le désir s'active quand un stimulus signale la précision que la policy mène à la récompense (Schwartenbeck et al., 2015) et est influencée par les états physiologiques (Berridge, 2012), notre seconde stimulation contribue à expliquer comment le besoin amplifie le désir. Spécifiquement, les états de besoin ou états surprenants signalent une forme d'entropie qui influence l'état physiologique, et qui impacte la réactivité de la dopamine mésolimbique. Cela fait en sorte que les signaux de récompense déclenchent la production de la dopamine qui, étant déjà très réactive, attribue une plus grande saillance motivationnelle, c'est-à-dire une plus grande précision, à ces signaux de récompense, car ils réduisent l'entropie. Ainsi, le désir généré est amplifié lorsqu'un stimulus fournit un chemin vers l'état préféré. L'entropie étant l'incertitude sur quel état occuper, la présence de l'état préféré réduit cette incertitude, car l'animal « sait » quel état occuper. Par conséquent, les signaux qui indiquent, ou sont sur, le chemin vers cet état préféré renforcent cette certitude (précision).

Il existe plusieurs formes de précisions, et les états de besoin n'amplifient ces précisions que s'ils sont présents dans l'environnement

Le fait qu'il existe différentes précisions associées à différentes prédictions (Parr et al., 2022) signifie que les états de besoin influencent la valeur des stimuli et des actions en fonction de ce qui est présent dans l'environnement. Par exemple, en état de besoin, la présence d'un signal qui prédit que la policy mène à la récompense à venir peut amplifier le désir, mais la sensation directe de la récompense elle-même va amplifier le plaisir ; et la simple perception de la récompense peut causer un changement dans la prédiction intéroceptive. Ceci explique pourquoi, parfois, le besoin amplifie le désir, et parfois non : le besoin amplifie la précision de différents stimuli selon ce qu'ils prédisent dans un contexte donné. Par exemple, pour que le besoin (entropie) amplifie le plaisir, il faut que le corps entre en contact avec la récompense. On ne peut pas ressentir le plaisir de la nourriture simplement parce qu'on a faim. De la même manière, on

peut imaginer que pour que le besoin amplifie le désir, il faut que le stimulus puisse indiquer que la policy mène à la récompense, ce qui expliquerait nos résultats de l'étude 2. En effet, la deuxième étude l'illustre en montrant que lorsque les participants voyaient passivement des images de nourriture, même s'ils avaient faim, il n'y avait pas d'activation consistante du système dopaminergique et donc pas d'amplification du désir, car les images de la nourriture ne leur signalaient pas que dans la séquence d'événements, ils recevraient la nourriture. Toutefois, cette vision passive conduisait néanmoins à une activation dans l'insula mi-postérieure, probablement parce que ces stimuli signalaient toujours une précision sur la prédiction interoceptive (« je suis en manque de ceci » ; « ceci pourrait changer mon état interne ») même s'ils ne signalaient pas une précision sur la policy (« je dois me préparer à recevoir ou à obtenir ceci »). L'interprétation que le besoin peut amplifier la précision d'un stimulus dont la signification est liée au changement dans la prédiction interoceptive actuelle est en lien avec les récentes théories sur la prédiction interoceptive (Barrett et Simmon, 2015), qui a été démontrée expérimentalement (Livneh et al., 2016 ; Livneh et al., 2020).

CONCORDANCE ENTRE BESOIN ET DÉSIR

Le besoin et le désir peuvent être synchronisés (concordance), et dans ce cas le besoin amplifie le désir. L'article 3 l'a démontré : les résultats de la simulation montrent que la présence conjointe d'états biologiquement coûteux et d'un chemin vers l'état préféré réduit l'entropie et augmente la précision, et plus les états surprenants sont coûteux, plus l'agent ou l'animal est certain qu'il doit aller vers l'état préféré. Ceci explique comment les états de besoin amplifient le désir, ou même le plaisir, la réaction interoceptive, etc. : cela est dû au fait que les stimuli y étant liés réduisent l'entropie ou plus clairement, ils précisent le chemin vers l'état préféré. Aussi, les résultats de l'article 1, qui indiquent que le réseau cérébral de conjonction entre stimuli physiologiques et sociaux dont on est privé est corrélé à la distribution du récepteur 5HT4 de la sérotonine, pourraient expliquer en partie comment l'état de besoin influence le désir en modulant l'activité des neurones de la sérotonine. En effet, le VTA est modulé par les neurones du noyau dorsal de raphé (DRN) (Gervais & Rouillard, 2000), dont l'activité, comme le suggèrent notre étude 1 et la littérature (Rebholz, et al., 2018 ; Takagishi and Chiba 1991 ; Peyron et al., 1998 ; Lucas et al,

2005 ; voir aussi Price, 2007 ; Weston, 2012 ; Castello, et al 2018 ; Geddes et al.2016), est régulée par la portion prélimbique (« pregenual ») de l'ACC via le récepteur 5HT4. En ce sens, nos résultats fournissent une explication possible du mécanisme sous-jacent à l'amplification du désir par les besoins physiologiques ou sociaux (voir Tomova et al., 2020). Plus spécifiquement, via 5HT4, l'ACC régulerait le DRN sérotoninergique, qui à son tour influencerait l'activité dopaminergique du VTA/SN. En outre, l'amplification ou modulation du désir par les états de besoin se produirait également par l'influence directe et indirecte de l'hypothalamus ou de l'insula sur les régions dopaminergiques et le noyau central de l'amygdale (Liu et al., 2020 ; Choudhary et al., 2018 ; Beier et al., 2015 ; Balleine, 2005 ; Ponsérre et al., 2020).

DISCORDANCE ENTRE BESOIN ET DÉSIR

S'il y a une discordance entre le besoin et le désir, c'est-à-dire que les deux peuvent s'appliquer de manière indépendante pour le même stimulus (ou action), cette discordance est double. D'une part, le besoin est lié aux tendances à occuper les états préférés, et est donc théoriquement indépendant des prédictions de récompenses qui sont liées au désir, comme démontré dans la troisième étude. Seuls les signaux et récompenses qui sont sur le chemin de cette tendance sont amplifiés par le besoin, car ils réduisent l'entropie et augmentent la précision. Cependant, cette amplification du besoin sur le désir (ou même sur le plaisir, le choix ou sur la réaction interoceptive) dépend du contexte, soit de ce que les stimuli prédisent (interception versus récompense, etc.). En ce sens, comme mentionné, pour que le besoin amplifie le désir, il faut la présence d'un stimulus qui prédit que la policy mènera à la récompense. Ainsi dans la deuxième étude, le besoin n'a pas suffisamment activé le système dopaminergique parce que les stimuli perçus n'indiquaient pas suffisamment que dans la séquence d'événements, la récompense serait obtenue. D'autre part, le désir est généré par la prédiction de récompense, qui est liée à la précision sur les policies menant à la récompense, et est techniquement indépendante du besoin (Bindra, 1974 ; Berridge, 2004). C'est en ce sens que la deuxième étude a montré une activité consistante du système dopaminergique pour le désir, et ce, en l'absence de besoin. De plus, le désir peut être amplifié par d'autres états que le besoin, comme les émotions, le stress, la drogue,

etc. (Berridge, 1996 ; Berridge, 2004); ce qui laisse suggérer que les états de besoin ne sont peut-être pas les seuls à générer l'entropie ou à influencer la réactivité du système dopaminergique. C'est ainsi qu'il peut y avoir besoin sans désir, et désir sans besoin.

DIFFÉRENCE FONDAMENTALE QUI EXPLIQUE LA CONCORDANCE ET LA DISCORDANCE ENTRE BESOIN ET DÉSIR

L'une des idées principales de cette thèse était que les différences entre besoin et désir liées à leurs natures théoriques permettraient d'expliquer pourquoi parfois il y a discordance et concordance entre ces deux états. En effet, il y a une différence fondamentale entre besoin et désir, en particulier dans la manière dont ils orientent le choix ou la sélection d'action, c'est-à-dire la policy ; et c'est cette différence qui permet de comprendre la discordance et la concordance. Dans le cas du besoin, la policy vient avant la récompense. En d'autres termes, la tendance à aller vers l'état préféré active une policy, et les récompenses sont les stimuli ou actions qui sont sur la trajectoire de cette policy. Tandis que pour le désir, c'est l'inverse : la récompense vient avant la policy ; et c'est la prédiction de la récompense qui détermine quelle policy espérer ou poursuivre dans le but d'obtenir la récompense. Cette différence de préséance entre policy et récompense peut être due au fait que dans le cas du besoin, il s'agit de policy interne, liée au fonctionnement de l'organisme, par homéostasie ou allostasie, et possiblement aux comportements liés au système autonome ou neuroendocrinien. Tandis que pour le désir, il s'agit de policies externes, c'est-à-dire celles liées aux changements de l'environnement, lesquelles peuvent être influencées par les comportements « externes » émis par le système moteur somatique de l'individu. C'est d'ailleurs pour cela que le désir possède plus de contrôle sur la portion activationnelle de la motivation que le besoin. Le fait que pour le besoin, la policy vienne avant signifie aussi que, dans le cas du besoin, la policy interne influence ou détermine la récompense alors que dans le cas du désir, la récompense influence ou détermine la policy externe. Ainsi, si la récompense déterminée par le besoin, c'est-à-dire, en lien avec la policy interne, est la même que la récompense prédite par un signal de récompense qui précise la policy

externe, alors il y aura concordance ; sinon il y aura discordance. Par exemple, la soif déclenche des changements hormonaux et neuronaux, et la nature de ces changements peut être considérée comme une policy interne poussant l'animal vers l'état préféré, et ce, de manière directionnelle : vers la satiété de la soif et non celle de la faim ou de la solitude, etc., et les stimuli menant à l'état préféré deviennent des récompenses, comme l'eau dans ce cas. Ainsi, lorsqu'un animal assoiffé et relativement non affamé perçoit un signal de nourriture, il sera probablement motivé à suivre ce signal, car il y a une probabilité de nourriture, surtout si celle-ci est relativement rare. Cependant, si cet animal perçoit un signal d'eau, il sera motivé non seulement parce qu'il y a une probabilité d'eau, mais surtout parce que cette eau sera très gratifiante puisqu'elle le mènera à l'état préféré dont il est éloigné. En d'autres termes, l'état de besoin n'amplifie pas la précision de la policy parce que celle-ci mène à la récompense, mais il amplifie la précision de la policy parce que la récompense au bout de cette policy sera une « vraie » récompense. C'est dans ce sens que le besoin amplifie le désir ; et ainsi, il y a concordance (association) lorsque la récompense déterminée par le besoin est la même que celle prédite, sinon il y a discordance (dissociation).

SECTION VI : FORCES ET LIMITES

Cette thèse se démarque par ses méta-analyses qui sondent ce qui est commun aux besoins physiologiques et sociaux. Pour distinguer le besoin du désir, elle utilise des méthodes novatrices, notamment la combinaison de l'imagerie cérébrale et des neurosciences computationnelles. En effet, elle compare dans le cerveau les patrons d'activation liés au besoin versus au désir, en compilant un éventail de plusieurs études en neuroimagerie, et ce, de manière quantitative par le biais de méta-analyses. Elle utilise également des outils mathématiques et computationnels afin de modéliser la différence entre besoin et désir et lui donner une assise théorique. Ces approches sont plus probantes comparativement à une approche purement philosophique pour discuter des besoins et des désirs, car elles permettent d'avoir une assise biologique et mathématique.

Une des limites est que premièrement, il aurait fallu y intégrer plusieurs autres disciplines qui étudient différents aspects des besoins et des désirs. Toutefois, le choix des outils utilisés a permis de partir de la source, le cerveau, et de développer des idées pouvant s'étendre et s'utiliser dans d'autres domaines. Dans le même ordre d'idées, les types de besoins et de désirs présentés sont loin d'être exhaustifs ; et de plus, les circonstances dans lesquelles les besoins et les désirs sont définis dans la thèse n'englobent pas toutes les circonstances possibles. Par exemple, la notion introduite ici de « coût biologique », bien qu'intéressante, a des limites : tous les besoins sont-ils liés à un coût biologique si on n'y répond pas ? On peut penser à des besoins liés à la reproduction, par exemple. Une autre limite vient du fait que les concepts de « besoin » et « désir » ainsi que d'autres qui leur sont liés (« préférence », « motivation », etc.) existent dans le langage depuis des millénaires, bien avant l'arrivée des neurosciences. En ce sens, il est possible que ce qui se passe dans le cerveau soit loin de la démarcation entre ces concepts imposée par le langage. Ainsi, cette thèse comporte plusieurs limites qui pourraient être adressées dans de futures recherches.

SECTION VII : PERSPECTIVES ET RETOMBÉES

Cette thèse comporte également plusieurs idées dont certaines sont nouvelles, et d'autres constituent des améliorations aux idées actuelles. Premièrement, elle apporte l'idée que le besoin est différent du désir dans une perspective nouvelle et profonde. L'une des confusions sur la distinction entre besoin et désir est qu'on ne sépare pas l'aspect « différence » de l'aspect « concordance et discordance » (ou « association et dissociation »). En mettant ces deux aspects au clair, cette thèse a permis de distinguer les manifestations des besoins et des désirs, notamment dans le cerveau, avec l'insula mid-postérieure pour le besoin et les régions liées à la dopamine mésolimbique (VTA et NAcc) pour le désir. Aussi, la thèse introduit la notion d'effet « sous-jacent » du besoin, et la distinction entre la policy interne et externe, lesquelles permettent d'expliquer pourquoi le désir contrôle plus l'activation du comportement, mais que le besoin peut moduler le désir tout comme il peut moduler le plaisir, le choix, etc., et ce, autant dans le cerveau que dans le comportement, notamment avec l'effet directionnel du besoin et l'effet à la fois activationnel et directionnel du désir. La thèse introduit également la notion « d'entropie liée au besoin », et la possibilité que d'autres phénomènes puissent causer l'entropie et exciter le désir, ce qui est cohérent avec la théorie de la saillance incitative (voir Berridge, 2004). On trouve aussi dans cette thèse l'idée de coûts biologiques pour définir l'état de besoin. Cette notion est importante, car toutes les tendances innées ne sont pas nécessairement liées à des coûts biologiques ; on peut penser à certains comportements ou préférences liés à la sélection sexuelle. En outre, ce projet sur la « différence entre le désir et le besoin » pourrait avoir plusieurs retombées. En effet, les besoins, désirs et motivations étant à la base de plusieurs comportements humains, la question de recherche a une valeur scientifique, philosophique et sociétale évidente. Une partie des retombées sur le plan scientifique est de permettre une compréhension accrue des comportements économiques et sociaux. Par exemple, les états préférés peuvent être également conceptualisés comme des « modes », tant au sens statistique que profane du terme. Ainsi, les politiques publiques qui visent à intervenir sur des populations en considérant leurs besoins et désirs (McGregor et al., 2009) pourraient tenir compte des modes de vie des populations concernées, sous l'angle d'état préféré comme discuté ici. Finalement, une autre des retombées importantes concerne les comportements mésadaptés liés à la consommation excessive, comme

dans le cas des dépendances aux drogues. Il serait important de se poser la question de savoir si la personne consomme par besoin (dépendance) ou désir (addiction) (voir O'Brien et al., 2006). Selon le cas, il est possible de cibler des régions de cerveau différentes. Par exemple, selon le cas, faut-il plus intervenir au niveau de la prédiction de récompense et de la dopamine ou au niveau de l'interoception et de l'insula ou la sérotonine ? Ce questionnement permettrait des approches ciblées dans la sphère de l'intervention sociale, afin d'aider les personnes affectées à modifier positivement leurs comportements. En outre, le lien entre l'état de besoin, l'insula et la sérotonine pourrait contribuer à la compréhension de phénomènes tels que la dépression et l'anxiété.

SECTION VIII : CONCLUSION

Dans cette thèse, nous avons appris qu'il y a une différence entre besoin et désir dans leurs patrons d'activation cérébrale ainsi que dans leurs natures théoriques. Cette différence permet d'expliquer pourquoi, parfois, il y a concordance et, parfois, il y a discordance entre besoin et désir. Les résultats suggèrent que, dans le cerveau, la différence serait que le besoin est plus relié à l'activité de l'insula mi-postérieure, qui attribue la valeur aux stimuli relativement à leur impact sur l'état interne actuel et futur. Tandis que pour le désir, les résultats indiquent qu'il est lié aux régions centrales de la dopamine mésolimbique, notamment le VTA et le NAcc, qui attribuent la valeur aux stimuli relativement à la prédiction de récompense, et activent le comportement pour atteindre cette récompense. Les méta-analyses effectuées ont également montré que ces deux types de valeurs s'appliquent de manière indépendante, d'où le fait que le besoin et le désir peuvent être associés (concordance) ou dissociés (discordance). La raison pour laquelle cette possibilité arrive dépend de leurs natures théoriques, qui fait que le besoin a un effet sous-jacent qui peut influencer le désir ; mais cette influence peut se manifester ou non selon les contextes. En effet, le besoin tire son effet sous-jacent de la tendance des êtres vivants à occuper leurs états préférés afin de réduire l'entropie. Allant dans ce sens, les résultats de la première simulation ont montré que cette tendance attribue de la valeur aux stimuli (et actions) qui mènent à l'état préféré, et augmente par rapport à l'état de besoin, et ce, indépendamment du

désir. Ce dernier est lié aux stimuli qui signalent une certitude (précision) que la policy mène à la récompense, et ce, indépendamment du besoin. Les résultats de la seconde simulation computationnelle ont montré comment l'état de besoin amplifie la précision du signal de récompense. En ce sens, le besoin amplifie la certitude que la récompense au bout de ce désir est une 'vraie' récompense, car elle mène à l'état préféré. Ainsi, le besoin et le désir sont en concordance lorsque le stimulus qui mène à l'état préféré est également la récompense prédite, c'est-à-dire celle à laquelle mène la policy. Le fait d'avoir utilisé l'imagerie cérébrale pour sonder ce qui est commun aux besoins et ce qui leur est propre par opposition au désir et vice versa, ainsi que d'avoir combiné cela avec des méthodes et théories computationnelles, a permis de développer une meilleure compréhension de la différence entre besoin et désir et sur comment ils interagissent : s'associent et se dissocient. Cette distinction pourrait être utile en matière d'intervention sociale ; par exemple en ce qui concerne la consommation et ce, tant pour un individu que pour un groupe ou une société.

SECTION VI : RÉFÉRENCE BIBLIOGRAPHIQUE

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