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Distinct neural representations of perceptual and numerical absence in the human brain

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eLife Assessment

This **valuable** study presents evidence that the human brain encodes perceptual absence and numerical absence through distinct neural codes, while confirming that symbolic and non-symbolic forms of zero share a common representation. The evidence supporting this dissociation is **convincing**, drawing on neural decoding techniques and Bayesian analyses, although some concerns remain about task design and decoding method, which could partly explain the lack of shared representation. The work will be of interest to neuroscientists and psychologists studying numerical cognition and the boundary between perception and higher-level cognition.

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Abstract

The ability to represent absences is fundamental to human perception and cognition. Sensitivity to perceptual absences depends on inferring a lack of sensory evidence, enabling the recognition of a lack of environmental resources or other objects. In turn, encoding absence as a concept – in the form of the number zero - has enabled a multitude of technological and mathematical advances. Whether perceptual and conceptual absences rely on overlapping or distinct neural representations in the human brain, however, remains unknown. We employed three different tasks together with magnetoencephalography (MEG) to characterise neural representations of absence evoked within perceptual and numerical domains. Using multivariate decoding and Bayes factor analyses, we replicate previous findings of shared representations of numerical absence across symbolic and non-symbolic formats. In contrast, we show that these representations of numerical absence are distinct to those evoked by perceptual absences. This result held even after controlling for stimulus-level confounds which generate surface-level similarities between perceptual absences and non-symbolic empty sets. Our results extend a boundary between perception and cognition to the domain of absence and provide insight into the different mechanisms employed by the human brain to both perceive and conceive of absences.

Introduction

When describing the central tenets of jazz, Miles Davis said “It’s not the notes you play, it’s the notes you *don’t* play.” With this aphorism, he distilled a fundamental insight that perceptions of absence are core features of sensory experience. Just as we can recognise a friend in a crowded café, we can also notice their absence if they are late; just as we are aware of the birds calling outside our window, we can become aware of the silence once they stop. The perception of absence also has conceptual significance, indicating the lack of countable items in a set. Ultimately,

the ability to represent absence as a symbolic, numerical concept underpins the emergence of the number zero in mathematics – a fundamental advance in human culture underpinning a range of technological and scientific advances (Kaplan, 1999).

How these two types of absence – perceptual and conceptual - are inter-related psychologically and neurally remains poorly understood. On the one hand, it has been hypothesised that the conceptual representation of zero is continuous with a more fundamental and primitive representation of perceptual absence (Barton, 2020; Nieder, 2016). This hypothesis stems from findings of delayed mastery of both perceptual (Coldren & Haaf, 2000; Sainsbury, 1971) and numerical (Wellman & Miller, 1986; Wynn & Chiang, 1998) absences across development, and observations that children appear to scaffold the zero-concept onto notions of nothingness or absence when learning zero's place at the start of the number line (Bialystok & Codd, 2000; Krajcsi et al., 2021). In adults, behavioural performance is often impaired for tasks involving zero compared to positive numbers (Brysbaert, 1995; Kutter et al., 2023) and this is mirrored in perceptual absences, where reaction times are often longer for stimulus-absence than stimulus-presence decisions (Kellij et al., 2021; Mazor et al., 2020, 2025; Meuwese et al., 2014). On the other hand, a tradition in perception science recognises a boundary between perception and cognition, whereby perceptual and conceptual representations are distinct (Block, 2023; Firestone & Scholl, 2016). Applying this framework to the case of absence, we might expect that inferring perceptual absences – such as recognising a lack of birdsong – may be achieved via using distinct mechanisms to those supporting a representation of conceptual (e.g. numerical) absences such as zero. However, beyond an initial period of perceptual scaffolding of numerical absences in childhood, it remains unclear whether the neural underpinnings of perceptual and numerical absence in the adult human brain are overlapping or distinct.

Perceptual absences have been shown to rely on dedicated neural machinery that are – at least in part – distinct from that underlying detection of stimulus presence. For example, in non-human primates, individual neurons in the prefrontal cortex specifically fire prior to reporting an absence of experience in a perceptual detection task (Merten & Nieder, 2012). Neurons with similar characteristics have also been found in the nidopallium caudolaterale of carrion crows (Wagener & Nieder, 2024), suggesting the active encoding of absence may be an evolutionarily preserved function that relies upon higher-order or associative brain regions. In line with this, single neurons in the posterior parietal cortex of humans show stimulus-locked responses to the failed detection of targets (Pereira et al., 2021). More generally, a capacity to self-monitor the reliability of perceptual systems may be important for distinguishing between bona fide perceptual absences and lapses in attention (Mazor et al., 2025).

Neural representations of the number zero show similarly distinct properties. Like perceptual absences, numerical absences are actively represented in higher-order brain regions of non-human primates (Okuyama et al., 2015; Ramirez-Cardenas et al., 2016) and crows (Kirschhock et al., 2021). Importantly, two different coding schemes seem to underwrite single-cell representation of zero. Some cells represent zero in a continuous manner, firing maximally for numerical absence and showing a graded decrease in activation as numerical magnitude increases (Okuyama et al., 2015; Ramirez-Cardenas et al., 2016). In contrast, other cells show an exclusive response profile, responding specifically to zero and being equally inactive for all other magnitudes (Okuyama et al., 2015; Ramirez-Cardenas et al., 2016), reminiscent of a categorical representation of "nothing" (vs. "something"). In humans, single cells in the medial temporal lobe have also been shown to encode numerical absence in both symbolic ("0") and non-symbolic (empty set) formats, with empty sets engaging partially distinct representations to countable numbers of dots at the population level (Kutter et al., 2024). Finally, in a previous study using MEG in humans, we recently identified neural representations of zero within human posterior parietal cortex which exhibited overlap between empty sets (i.e. blank squares) and symbolic zero (Barnett & Fleming, 2024).

Finding that conceptualisation of zero overlaps with representations of sensory absence would offer support to accounts that propose the evolutionary and developmental trajectory of zero concepts emerge from a more basic ability to track an absence of sensation (Nieder, 2016;

Barton, 2020). On the other hand, finding that neural representations of perceptual and numerical absences are distinct would support an extension of a boundary between perception and cognition into the domain of absence perception (Block, 2023; Firestone & Scholl, 2016). To decide between these possibilities, we recorded patterns of neural activation in both detection and numerical tasks using MEG. Participants either detected stimuli amongst noise or performed rapid calculations with dot patterns and numerical symbols. In each task, we extracted multivariate neural patterns that reliably tracked numerical and perceptual absence. We find that representations of numerical absence robustly generalise across symbolic and non-symbolic numerical formats, but do not generalise to perceptual absences. Together our findings provide evidence in favour of distinct neural representations of perceptual and numerical absence.

Results

Participants performed three tasks while undergoing MEG recording. They performed two numerical tasks which differed only in the format of numerical stimuli: non-symbolic dot patterns (empty sets to five dots) and symbolic numerals ("0" to "5"). In the numerical tasks, participants saw a rapid stream of 10 numbers, five of which were blue and five of which were orange (Figure 1A). At the end of the sequence, they reported whether the blue or orange set had a higher or lower average, counterbalanced across participants. In the perceptual task, participants were presented with a noisy grating at one of three calibrated SNR levels (Figure 1B; 1C). Participants were asked to report whether they saw the grating on each trial or not (Figure 1A). Using a range of SNR levels allowed us to gather an equal number of 'present' and 'absent' responses whilst controlling for stimulus contrast level (see *Decoding Analyses*). By relying on numerical and perceptual tasks that differed with respect to their structure and temporal dynamics, we were able to identify stimulus-locked neural representations of absence across different cognitive domains while controlling for differences in task-related responses (Barnett & Fleming, 2024).

Behaviour

In the perceptual detection task, participants were sensitive to the presence of the grating stimuli (mean d prime = 1.59, SD = 0.46, Figure 1D), while also showing a bias towards reporting the stimulus as absent (mean criterion = 0.91, SD = 0.34, Figure 1D). Replicating previous findings, participants took longer to report stimulus absence (mean RT = 0.32s, SD = 0.14s) compared to stimulus presence (mean RT = 0.28ms, SD = 0.11s, $t(28) = -3.0176$, $p = .0054$, Figure 1E). In the numerical tasks, participants were significantly above chance in reporting which stream had the higher average (symbolic: $t(28) = 20.61$, $p < .001$; non-symbolic: $t(28) = 23.53$, $p < .001$), and performance was similar between the symbolic and non-symbolic formats (mean symbolic accuracy = 0.73, SD = 0.06, mean non-symbolic accuracy = 0.73, SD = 0.5, $t(28) = -0.121$, $p = 0.90$).

Cross-Format Neural Representations of Numerical Absence

We first asked whether we could robustly identify neural activity patterns specific to numerical zero. We have shown previously using MEG that neural representations of numerical zero generalise between non-symbolic empty sets and symbolic zero (Barnett and Fleming, 2024). In line with this finding, binary decoders trained to discriminate zero vs. non-zero trials within each format revealed representations of zero that were decodable up to 800ms post-stimulus (Figure 2A, diagonal; Figure 2B, diagonal). By testing these decoders in the alternative numerical format, we examined whether neural representations of zero in one format generalise to the alternative format. We observed successful generalisation from around 200 to 800ms post-stimulus (train on non-symbolic: time averaged log10(BF) [0.2s, 0.8s] = 1.09; train on symbolic: time averaged log10(BF) [0.2s, 0.8s] = 0.74; Figure 2A, Figure 2B), replicating our previous findings of shared representations of zero across symbolic and non-symbolic numerical formats (Barnett and Fleming, 2024).

To determine whether these cross-format representations of zero exist on a graded neural number line, we used a one-vs-one decoding approach to compute the discriminability between zero and each non-zero numerosity in the alternative numerical format. Neural representations induced by

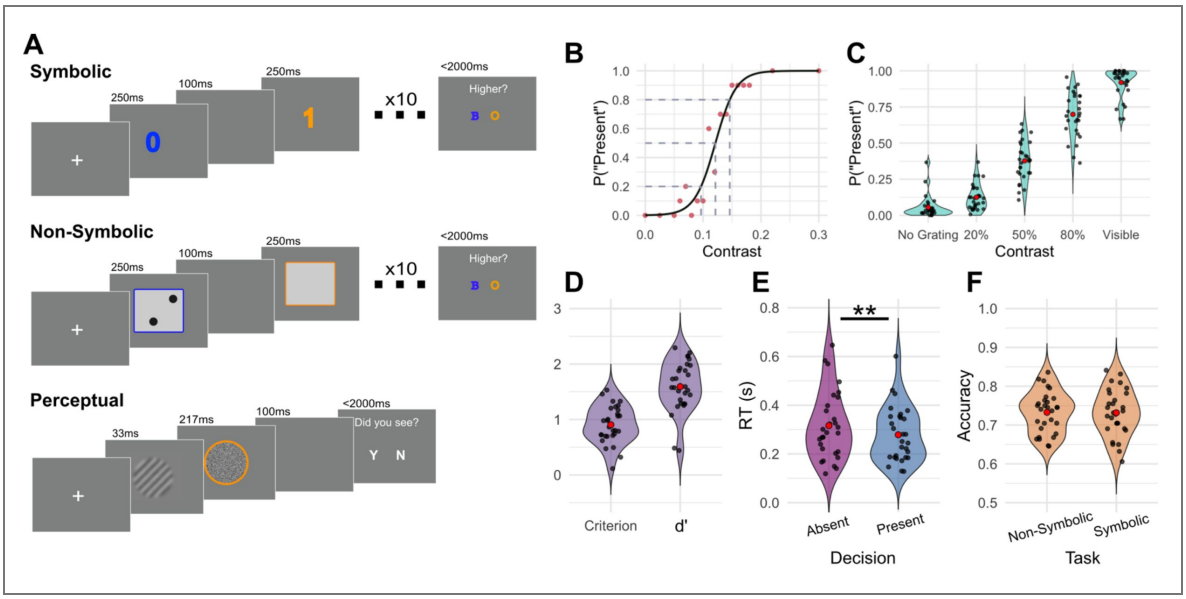


Figure 1. Tasks and Behavioural Performance.

A: Participants performed three tasks: two numerical (symbolic and non-symbolic) and one perceptual (detection). B: Example participant's psychometric function obtained during the calibration procedure. C: The proportion of gratings reported as 'present' in the detection task. In all subplots C-F, black dots are individual participants and red dots are the grand mean over all participants. D: Criterion and d' in the detection task. E: Reaction times for absent and present responses in the detection task. F: Accuracy in the symbolic and non-symbolic numerical tasks.

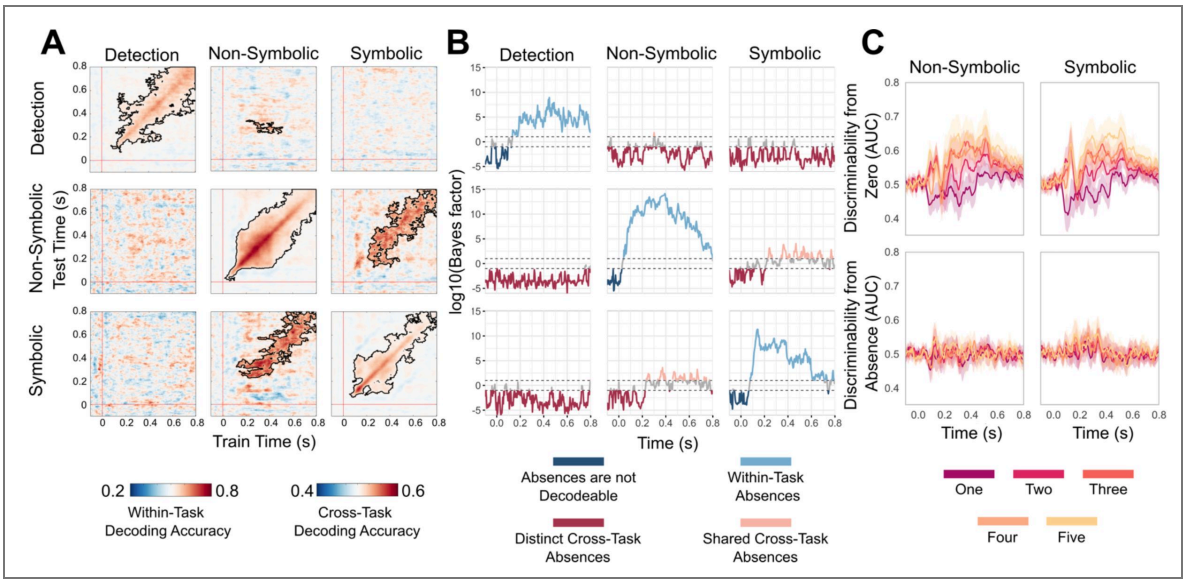


Figure 2. Distinct Representations of Perceptual and Numerical Absence.

A: Temporal generalisation decoding results. Representations of perceptual (top-left), non-symbolic (centre), and symbolic (bottom-right) absence were all decodable within each task, respectively. Numerical absences generalised across numerical formats (centre-right, bottom-centre) indicative of formatinvariant representations of numerical zero. Representations of perceptual absence did not generalise to numerical tasks, except for a small cluster of significant decoding when the perceptual absence decoder was tested on non-symbolic empty sets (top-right). Black outlines represent areas of significant decoding as computed by cluster-based permutation tests. *B*: Bayes factor analyses on diagonals of temporal generalisation matrices from *A*. log10(Bayes factors) above 1 indicate strong evidence for above chance decoding and those below -1 indicate strong evidence for chance-level decoding. Black dotted lines indicate this threshold for strong evidence in both directions. There was decisive evidence for decoding of absences within each task (light blue). There was very strong evidence for shared representations of absence between symbolic and non-symbolic formats (pink). There was very strong evidence for distinct representations of perceptual and numerical absence (red). *C:* Top: training a decoder to classify non-symbolic empty sets from non-symbolic numerosities and testing it on symbolic numbers in a one-vs-all process revealed increasing discriminability as distance from zero increased (left). The same cross-format distance effect is observed when training a classifier on symbolic zero and testing it on non-symbolic numerosities (right). Bottom: there was no evidence for larger numerosities being more discriminable from perceptual absence than smaller numbers in either the non-symbolic (top) or symbolic (bottom) task. Shaded areas represent 95% CIs.

non-symbolic zero (empty sets) were more often confused with the symbolic numeral 1 or 2 than they were with symbolic numerals 4 or 5 (Figure 2C, top-left). Equally, neural representations of symbolic zero ("0") were more often confused with one or two dots in the non-symbolic task, than they were with four or five dots (Figure 2C, top-right). Pairwise clusterbased permutation tests comparing the discriminability of different non-zero numerosities over time revealed clusters of significant differences in discriminability, where an increased distance from zero increased discriminability from cross-format zero (symbolic: 2 vs 1, cluster p = .002; 3 vs 2, p = .003; 4 vs 3, p = .15; 5 vs 4, p = .014; non-symbolic: 2 vs 1, cluster p = .001; 3 vs 2, p = .001; 4 vs 3, p = .27; 5 vs 4, p = .005). These analyses confirm a graded representation of numerical absence that is evoked by both non-symbolic empty sets and symbolic zero (Barnett & Fleming, 2024), and establish that we are able to robustly recover neural representations of numerical absence in our paradigm using MEG.

Neural Representations of Perceptual and Numerical Absence are Distinct

We next asked whether representations of absence are shared between perceptual and numerical domains. We first trained a decoder to discriminate MEG signals corresponding to 'absent' vs. 'present' responses in the perceptual detection task, independent of stimulus contrast (*see Decoding Analyses in Methods*). This allowed us to isolate neural representations underpinning inferences on perceptual absence while controlling for the influence of stimulus factors. Representations of perceptual absence were identified from 200ms to 800ms post-stimulus (Figure 2A, top-left), with Bayes factors (Figure 2B, top-left) indicating strong evidence for successful decoding.

Having established successful decoding of both perceptual and numerical absences, we next asked whether the perceptual absence decoder could successfully discriminate zero from non-zero trials in the numerical tasks, and vice-versa. This approach offers an empirical test of whether neural populations underpinning perceptual absence reports are also recruited when calculating with numerical zero. To allow us to obtain evidence for or against shared representations of numerical and perceptual absence, we computed Bayes factors (BF) – with positive BFs indicating evidence in favour of generalised representations, and negative BFs indicating evidence in favour of distinct neural representations. To assist in visualisation, we plot log10 transformation of BFs such that BFs supporting either distinct or generalised representations are symmetric around zero. Interpretation of log10 BFs follows standard convention for interpreting BFs, with log10(BF) in the range [0, ±0.5] offering weak evidence, [±0.5, ±1] moderate evidence, [±1, ±1.5] strong evidence, [±1, ±2] very strong evidence, and [±2, ±inf] being decisive (Jeffreys, 1998). In our plots, we indicate the timepoints when evidence for either hypothesis exceeds the threshold for strong evidence.

We note that within each domain (perceptual and numerical) there was strong evidence for decoding of absences, suggesting any failure to generalise between domains is not due to a lack of signal (Figure 2B, diagonal). We also included a control feature – stimulus colour (orange vs. blue) – that was common to each of the three tasks (Fig. 1A). This feature showed both robust within-domain decoding, and, crucially, cross-domain generalisation for all pairwise combinations of tasks (Supplementary Figure 2) – suggesting that any failure to observe cross-domain generalisation of perceptual/numerical absence is not due to a general failure to identify shared neural signatures across the different task contexts.

Overall, when training decoders on the detection task and testing on the numerical tasks, BFs indicated decisive evidence in favour of the hypothesis of distinct representations of perceptual and numerical absence throughout the trial epoch (Figure 2B). This was the case for both the symbolic (time averaged log10(BF) [0.2s, 0.8s] = −2.91) and non-symbolic tasks (time averaged log10(BF) [0.2s, 0.8s] = −2.16). Training decoders in the alternative direction (i.e. training on numerical tasks and testing on the detection task) also supported a hypothesis of distinct neural representations of perceptual and numerical absence (Figure 2B) (symbolic: time averaged log10(BF) [0.2s, 0.8s] = −3.24; non-symbolic: time averaged log10(BF) [0.2s, 0.8s] = −3.44). The only exception to this general pattern was when generalising from a non-symbolic empty set decoder to

perceptual absences, which revealed a brief positive peak around 300ms post-stimulus consistent with evidence for shared representations; however, the time-averaged BF across the full 200-800ms window remained strongly negative, and in support of distinct representations (peak log10(BF) = 1.83, time averaged log10(BF) [0.2s, 0.8s] = −2.16) (Figure 2A, top-middle, Figure 2B, top-middle). We also established that pre-stimulus neural representations of perceptual and numerical absence identified in the alpha band were not shared between tasks (Supplemental Figure 3; Supplemental Figure 4).

If representations of absence are shared between perceptual and numerical domains, we would expect perceptual absences to show signatures of a neural number line, and be less discriminable from lower numerosities than higher numerosities. To test this, we again performed a one-vs-one cross-decoding analysis, where we tested our perceptual absence decoder (absent vs. present decision) on different pairs of zero and non-zero numerosities (i.e. 0 vs. 1; 0 vs. 2; 0 vs. 3; 0 vs. 4; 0 vs. 5). Again, in line with distinct neural representations of perceptual and numerical absence, larger numerosities did not show a significant increase in discriminability from perceptual absence when compared to either smaller non-symbolic numerosities (all *p*s > .157; Figure 2C, bottom-left) or symbolic numerals (all *p*s > .130; Figure 2C, bottom-right).

Visual Features of Perceptual Absences Generalise to Empty Set Stimuli

Taken together, our analyses indicate strong evidence (as derived from BFs) that neural representations of perceptual and numerical absence can be robustly identified in patterns of MEG activity, and that these representations are distinct rather than shared. As noted above, the one exception to this pattern was a small but significant cluster of activity around 300ms that indicated some shared representation of non-symbolic and perceptual absences (Figure 2A; Figure 2B). We considered that this exception may have been driven by uncontrolled shared variance in lower-level visual features of our detection and empty-set stimuli. For instance, previous work has shown that the spatial frequency of non-symbolic dot patterns covaries with numerosity and can drive early visual responses to non-symbolic stimuli in numerical tasks (Paul et al., 2022). Given that the stimuli within our detection task varied in grating SNR and therefore spatial frequency, we reasoned that similar effects may contribute to the brief cluster of generalisation observed between perceptual and non-symbolic stimuli. By explicitly attempting to decode the physical presence or absence of the grating (which up until now was controlled for in our analysis) we aimed to further characterise this component of visually-driven shared variance.

To evaluate this possibility, we trained a decoder to classify Hits vs. Correct Rejections within the detection task (Figure 3A). This decoder should be not only sensitive to the 'present' or 'absent' decision made by a participant, but also the physical presence (or absence) of a grating. To maximise sensitivity in this analysis, only trials within the supra-threshold contrast level were used to define Hits. We then tested this decoder on empty sets vs. non-zero dot patterns and found a cluster of significant generalisation between 100ms and 300ms, with the peak BF indicating evidence for shared neural signatures across the two tasks (peak log10(BF) = 3.25; time averaged log10(BF) [0.05s, 0.3s] = −0.82; Figure 3B, left). When decoding in the alternative direction (training on empty sets vs. non-zero dot patterns and testing on Hits vs. Correct Rejections), we observed similar patterns of generalisation, with evidence in favour of shared neural signatures between the two stimulus sets (peak log10(BF) = 4.45; time averaged log10(BF) [0.05s, 0.3s] = 0.82; Figure 3B, right). Taken together, this result suggests that visual features (for instance, covarying spatial frequency profiles) may spuriously drive cross-decoding of absence in perceptual and non-symbolic numerical domains, unless stimulus contrast is appropriately controlled for. It is therefore all the more striking that, despite the potential for uncontrolled stimulus driven contributions to cross-decoding, we find strong evidence against shared neural representations of perceptual and numerical absence (Figure 3B).

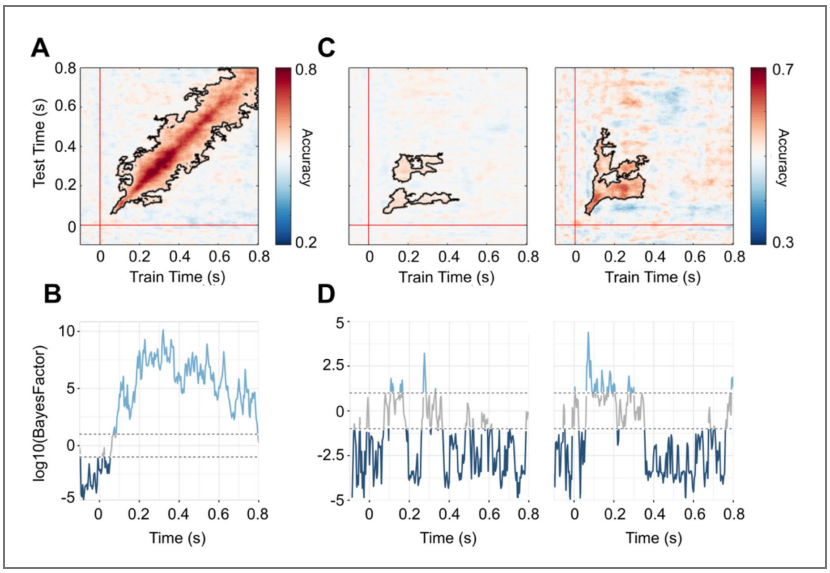


Figure 3. Stimulus Features Drive Generalisation Between Detection and Empty Set Stimuli.

A : A decoder trained to classify Hits vs. Correct Rejections could decode the presence and absence of grating stimuli from around 100ms after stimulus onset. *B:* Bayes factors exceeding the upper black dashed line (light blue) reflect strong evidence in favour of above-chance decoding. Bayes factors beneath the lower black dashed line (dark blue) reflect strong evidence in favour of chance-level decoding. *C:* Cross-decoding between grating presence and absence (*A*) and empty set vs. nonzero dot stimuli. *Left:* Training on the detection stimuli and testing on non-symbolic stimuli. A cluster of significant generalisation was observed between 100 and 300ms post stimulus onset. *Right* : Training on empty set vs. non-zero stimuli and testing on grating presence vs. absence in the detection task. Again, a cluster of significant cross-decoding was observed between 100 and 300ms following stimulus onset. *D: Left:* Bayes factors indicated moderate to strong evidence in favour of generalisation when testing on non-symbolic stimuli. *Right:* Bayes factors indicated strong evidence in favour of successful generalisation (light blue) when testing on perceptual presence vs. absence. Black outlines represent areas of significant decoding as computed by cluster-based permutation tests.

Discussion

Absences are fundamental to human consciousness and culture. Just as sensitivity to absences is pivotal for perception, the conceptualisation of absence as "zero" enabled technological advances ranging from accounting to astronomy (Kaplan, 1999). Yet how these two kinds of absence – perceptual and conceptual – are encoded in the brain, and specifically the extent to which they rely on shared neural representations, has remained unknown. One proposal holds that the brain scaffolds conceptual representations of absence on top of more basic sensory representations of absence (Barton, 2020; Nieder, 2016). An alternative view holds that perceptual and conceptual absences are distinct, and supported by separate neurocognitive resources (Block, 2023; Firestone & Scholl, 2016). Through a series of MEG decoding analyses, we provide evidence for the latter hypothesis, revealing distinct neural representations of absence in perceptual and numerical domains. Our findings extend previous proposals of a distinction between perception and cognition into the domain of absence perception and offer insight into the different mechanisms employed by the brain to both perceive and conceive of absences.

Whether perception and cognition can be demarcated according to the format of their representations is debated (Block, 2023; Quilty-Dunn, 2016; for review see Clarke & Beck, 2023). Classical distinctions describe perceptual representation as iconic, analogue, and non-propositional, while cognitive representations are thought to be conceptual and sentence-like (Block, 2023; Burge, 2018). Our data lend support to the thesis that conceptual and perceptual absences respect a boundary between perception and cognition. It is important to note, however, that the extent to which absences are in fact perceived remains debated. For instance, findings showing that absences do not 'pop out' in visual search tasks in the same way as presences (Treisman & Gormican, 1988) have been used to argue that absences are not represented in the visual system and that recognising an absence must always invoke some conceptualisation (Block 2023, p. 185). On the other hand, absences follow signatures of perceptual illusions (Goh et al., 2023; Phillips, 2013), with theoretical perspectives suggesting they are perceived either via inference (Mazor, 2025) or direct perception (Farennikova, 2013). A similar debate surrounds numerosity, in which approximate representations of non-symbolic numerosities have been argued to be perceptual, rather than conceptual (Burr et al., 2018; Burr & Ross, 2008). Our results shape this debate by revealing that neural representations of perceptual absence are qualitatively distinct from neural representations of both symbolic and non-symbolic numerical absences.

Perceptual and numerical absences are not the only kinds of absence represented in the brain. The capacity to know you don't know – or are unable to remember – something plausibly depends on the capacity to represent absences at a metacognitive level. In non-human primates, it has been shown that metacognition about absences of mnemonic evidence (i.e. decisions about one's own ignorance) rely on frontopolar cortex, while evaluating decisions about the presence of mnemonic evidence (i.e. decisions about the things one has seen) engages dorsolateral PFC (Miyamoto et al., 2018). One interpretation of this dissociation is that evaluating an absence of internal evidence requires an additional level of abstraction about one's own cognitive states that is not required when evaluating evidence in favour. Consistent with this proposal, medial frontopolar cortical activation in humans preferentially tracks confidence about reports of stimulus absence relative to reports of stimulus presence (Mazor et al., 2020). One intriguing possibility, therefore, is that the metacognitive evaluation of different absence experiences is served by a general abstraction process that recruits the frontopolar cortex. Whether or not such a system is required for evaluating decisions involving numerical absence remains to be tested.

Evidence from developmental studies indicates that the process of learning a zeroconcept involves a gradual mapping of numerical and verbal properties to notions of nothingness and absence (Nieder, 2016). For instance, even before children possess quantitative knowledge about zero's place on the number line, they can appreciate its relationship to 'no things' (Wellman & Miller, 1986) and even denote zero by leaving paper blank (Bialystok & Codd, 2000). Even after

quantitative knowledge of empty sets is established, however, meta-knowledge about zero's status as a number remains fragile (Krajcsi et al., 2021), illustrating the gradual emergence of a symbolic, numerical concept from a category of 'nothing.'

If zero is learned by mapping numerical concepts onto experiences of perceptual absence, then why do we find distinct representations of absence in the two domains? One explanation may be that, to master the linguistic and conceptual basis of zero, numerical representations of absence must be sufficiently abstracted away from sensory absences to be incorporated in a neural number line, ultimately resulting in distinct representations in the two cases. It has been suggested that the description of non-occurrences with positive labels can aid processing and memory of absence experiences (Hearst, 1991). Labelling nothingness with the word "zero" may therefore not only bring the concept into the realm of numbers but could also create a positive conceptual indicator for the presence of 'something', namely the presence of an absence. We anticipate that young children may exhibit stronger representational overlap between perceptual and numerical representations of absence during the development of conceptual understanding of zero.

Absences play a foundational role in human perception and culture. Here, we show that the adult human brain harbours distinct representations of perceptual and numerical absences. Despite representations of numerical zero generalising between non-symbolic empty sets and symbolic numerals, neither of these numerical representations generalised to representations of perceptual absence. This result held even when controlling for low-level stimulus confounds which we show can drive spurious generalisation between tasks. Taken together, our results reveal distinct neural substrates underpinning perceptual and conceptual absences and extend a boundary between perception and cognition to include cases of absences.

Methods

Participants

Thirty participants (M_{age}: 27.07 years, SD_{age}: 9.11) took part in the MEG experiment at the Department for Imaging Neuroscience, University College London. One participant performed at chance level in both numerical tasks and was therefore excluded from analyses. All analyses were performed on the remaining sample of 29 participants. Informed consent was given before the experiment and ethical approval was granted by the Research Ethics Committee of University College London (#1825/005).

Stimuli

The detection task involved participants detecting a grating patch embedded within Gaussian noise. Gratings were oriented 45° clockwise from vertical, contained 2 cycles per degree and subtended 3° of visual angle. The signal to noise ratio of the grating and Gaussian noise was adjusted to sample a range of values from each subject's psychometric function (see *Detection Calibration Procedure* below). The masks were noise patches that were randomly generated on each trial and contained either an orange or blue border.

Numerical dot stimuli were created using custom MATLAB 2021b (Mathworks) scripts and consisted of different numbers of dots (from zero to five) on grey backgrounds. Low-level visual properties of the stimuli (total dot area, density, luminance) did not covary with numerosity (Figure S1). Total dot area was controlled for by systematically reducing the size of the dots as the number of dots increased, such that the total number of pixels included in a stimulus were constant across numerosities. In both stimulus sets, 50% of dots were black and 50% were white, such that the contrast of the dot patterns did not increase with numerosity (the increase in contrast generated by an increasing number of black dots was cancelled out by the increased number of white dots). Figure S1 reports the correlation between these non-numerical features and numerosity in the non-symbolic stimulus set, highlighting how our stimulusgenerating procedure successfully controlled for the association between low-level visual properties and numerosity. Empty set stimuli contained only a grey background in both stimulus sets. To ensure

participants could not rely on low-level visual cues in identifying empty set stimuli, the background luminance was varied within and across stimulus sets and the background square size was randomly varied across all stimuli (between 150 and 250 pixels squared).

Experimental Procedure

The tasks were presented to subjects using MATLAB (Mathworks) and the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007). Participants practiced the tasks on a computer before the MEG session. In the MEG scanner, participants first performed a calibration procedure for the detection task (see *Detection Calibration Procedure* below). The tasks were then performed in alternating miniblocks of 60 detection trials, 22 symbolic trials and 22 non-symbolic trials per MEG recording block. The order of the tasks was pseudo-randomly ordered within each block, and the starting order was counterbalanced across participants. There were 10 MEG blocks in total, resulting in 600 detection trials, 220 symbolic numeral trials and 220 non-symbolic dot trials across the whole experiment. Participants responded using two buttons on a button box held in their right hand.

Symbolic Task

We modified the symbolic numeral averaging task introduced by (Spitzer et al., 2017) to include the number zero (Barnett & Fleming, 2024). In one trial, ten numerals ranging from zero to five were presented in a random order (Figure 1A; *Symbolic Zero*). Five of the numerals were blue and five were orange. Each numeral was displayed for 250ms with an interstimulus interval of 100ms. The numerals were randomly selected on each trial to obey the constraint that the mean of the blue numerals could not equal the mean of the orange numerals. The response required at the end of each trial was counterbalanced across subjects, with half of the subjects reporting which set of numerals (orange or blue) had the highest average, and the other half reporting which set had the lowest average. Participants had 2000ms to respond, after which they were given feedback in the form of a green (correct) or red (incorrect) rectangle surrounding the response options. The button-response mappings were counterbalanced across blocks to prevent motor information contaminating our decoding analyses. Intertrial intervals were randomly sampled from a uniform distribution between 600-1000ms.

Non-Symbolic Task

The non-symbolic task followed the same procedure as the symbolic task (Figure 1A; *Non-Symbolic*). The only difference was that, instead of seeing symbolic numerals, participants saw a stream of 10 dot patterns, five of which had an orange border and five had blue borders. The rest of the procedure was identical to the symbolic numeral task.

Detection Calibration Procedure

When participants were set up in the scanner, they first performed a calibration block for the detection task. The trials followed the same protocol as the detection task. A grating was presented for 33ms and was followed by a 217ms backward mask consisting of Gaussian noise (Figure 1A; Sensory Absence). Following stimulus presentation, participants reported whether they saw the grating or not. A total of 17 SNR values were sampled from 2.5% to 30%, with 10 trials per SNR. 20 additional pure noise trials were included, where no grating was presented. This process allowed us to fit participants' psychometric functions (Figure 1B), observing the SNR values where participants had the probability of detecting a stimulus 20%, 50%, and 80% of the time.

Detection Task

The detection task followed the same task structure as the calibration block (Figure 1A; Sensory Absence). Within each experimental block, 10% of trials were no-stimulus catch trials where no grating was presented. On another 10% of trials, we presented grating stimuli above threshold (30% SNR). The remaining 80% of trials were evenly split between SNR values computed from the calibration block (P(Present) = [20%, 50%, 80%]). Within each block there were 16 trials per each

SNR value (Figure 1C). The colour border to the backward masks was irrelevant to the task and participants were instructed to ignore the colours. Button response mappings were counterbalanced over blocks.

MEG Preprocessing

MEG data were recorded continuously at 600Hz using a 273-channel axial gradiometer system (CTF Omega, VSM MedTech) while participants sat upright inside the scanner. To remove line noise, the raw MEG data were preprocessed with a Discrete Fourier Transform and bandstop filter at 50Hz and its harmonics. A high pass filter of 0.5Hz was also applied to the data.

MEG data were analysed using FieldTrip (Oostenveld et al., 2011) and MVPA-light (Treder, 2020). The numerical tasks were segmented into epochs of −500ms to 4000ms relative to trial onset. For the detection task, segments were specified from – 400ms to 1500ms. Baseline correction was performed where, for each trial, activity in a pre-trial window (numerical: [–500, 0]ms, detection: [–200, 0]ms) was averaged and subtracted from the entire epoch per channel. Data were downsampled to 300Hz. During artefact rejection, trials with high kurtosis were visually inspected and manually removed if they were judged to contain excessive artefacts. An independent components analysis was carried out on the MEG data, and the components with the highest correlation with eye-tracking data were discarded after visual inspection. Components showing topographic and temporal signatures typically associated with cardiac artefacts were also removed by eye. This procedure was performed separately for the three tasks. Finally, a second stage of epoching was performed. In the numerical task, trials were segmented into -100ms to 800ms epochs around the onset of each numeral. Trials were then baseline corrected again using the pre-stimulus window. In the detection task, trials were segmented into -100ms to 800ms around target onset.

Decoding Analyses

To test whether representations of absence were shared between conceptual and perceptual domains, we used a series of decoding analyses. First, to reveal the temporal profile of format-specific and format-invariant representations of numerical zero, we trained a binary Linear Discriminant Analysis (LDA) decoder to decode zero vs. non-zero symbols and numerosities (Figure 2A). This was conducted using a temporal generalisation approach whereby a classifier is trained on each time point and tested on all other time points (King & Dehaene, 2014), revealing how stable neural representations are over time.

Within-format decoding involved training and testing a classifier to identify numerosities on trials from one format (e.g. numerals or dots). In cross-format decoding, we trained the classifier on one format and tested it on the other (e.g., training on symbolic trials and testing on non-symbolic trials, and vice versa). Importantly, cross-format decoding allows us to empirically assess whether neural patterns associated with different numerosities share a common neural code across formats. For statistical inference on within-task decoding, we conducted 5-fold crossvalidation. Cross-validation is not required in cross-format decoding because the test data are never seen by the classifier during training, and thus there is no risk of overfitting. In both analyses, prior to decoding, the non-zero numerosities were balanced and five trials per numerosity were averaged. Next, zero and non-zero numerosities were balanced. The resulting ‘zero’ decoders were uniquely trained to identify neural representations of numerical zero in symbolic or non-symbolic format (Figure 2A). As such, when tested on the alternative format, any successful crossdecoding is evidence for format-invariant representations of zero.

Next, we used binary decoders to reveal whether abstract representations of numerical zero exist on a graded number line. Here, we trained the decoders to discriminate zero vs. all non-zero numerosities (one to five) separately and then tested these binary decoders on the corresponding numerosities in the opposite format (Figure 2B). This resulted in five different classifiers per format (Barnett & Fleming, 2024). This was done in both decoding directions: training on non-symbolic trials and testing on symbolic numerals; training on symbolic numerals and testing on non-symbolic trials. We used the area under the receiver operating characteristic (AUROC) as a

metric for discriminability between each pair of classes. In line with the hypothesis that format-invariant representations of zero exist on a graded, abstract neural number line, we expected discriminability to improve as numerical distance from zero increased. To test this effect statistically, we performed one-tailed, paired comparisons between the discriminability of successive numbers with zero (e.g., by comparing 0-2 vs. 0-1, 0-3 vs. 0-2, etc.).

To examine whether representations of absence were shared across numerical and sensory domains, we trained a binary decoder to classify participants' Hits (where a stimulus is presented and the participant reports 'present') vs. Misses (where a stimulus is presented and the participant reports 'absent') in the detection task (Figure 3A). Stimulus-absent and above-threshold trials were removed from this analysis. An equal number of Hits and Misses were used from each of the other three SNR values used in the experiment. As such, there was equivalent stimulus information across trials with 'present' and 'absent' responses, limiting the contribution of low-level visual features contributing to the decoding of neural correlates of perceptual detection. This decoder was then tested on the two numerical tasks, which again had been sorted into zero and non-zero trials (Figure 3B). Decoding was done in both directions (training on detection, testing on numerical tasks, and vice versa). Similar to the analysis examining whether cross-format representations of zero were graded, we took the Hits vs. Misses decoder and tested it on individual pairs of numbers (e.g. 0-1, 0-2, etc.) in both numerical formats (Figure 3C). If sensory absence shares representational properties with numerical zero, we would expect to see greater discriminability of larger numbers from sensory absence than smaller numbers. Again, to test whether this was the case, we performed one-tailed, paired comparisons between the discriminability of successive numbers with sensory absence (e.g., by comparing absence-2 vs. absence-1, absence-3 vs. absence-2, etc.).

Previous work has found neural activity in the alpha band to predict reports of stimulus presence and absence (Mathewson et al., 2009; Samaha et al., 2017). To extract alpha band activity from our data, we bandpass filtered our continuous, unepoched data between 8 – 12Hz and performed a Hilbert transform. Taking the absolute value of the Hilbert transformed data returned the amplitude of the alpha band signal over time, which could then be used as input to our decoder in the same way as analyses described above used the broadband MEG signal. The same trials were removed from analysis as those identified in the initial visual artefact rejection procedure. The same cross-decoding analyses were then performed on the alpha amplitude data, testing decoders within each task (Hits vs. Misses; Empty Sets vs. Non-Zero Dots; Symbolic Zero vs. Non-Zero Numerals) and across tasks (Supplemental Figure 3; Supplemental Figure 4).

Finally, to test whether low-level visual features of empty set and grating stimuli drive similar neural activity, we trained a decoder to discriminate stimulus-absent trials from above-threshold trials (Correct Rejections vs. Hits) in the detection task and tested this on empty set and non-zero dot patterns (and vice versa) (Figure 4).

For all decoding analyses, we used binary LDA decoders in conjunction with the MVPA-light toolbox (Treder, 2020) integrated with FieldTrip. To improve the robustness of the classifier, we applied L1-regularization to the covariance matrix, and the shrinkage parameter was automatically determined using the Ledoit-Wolf formula within each training fold (Ledoit & Wolf, 2004).

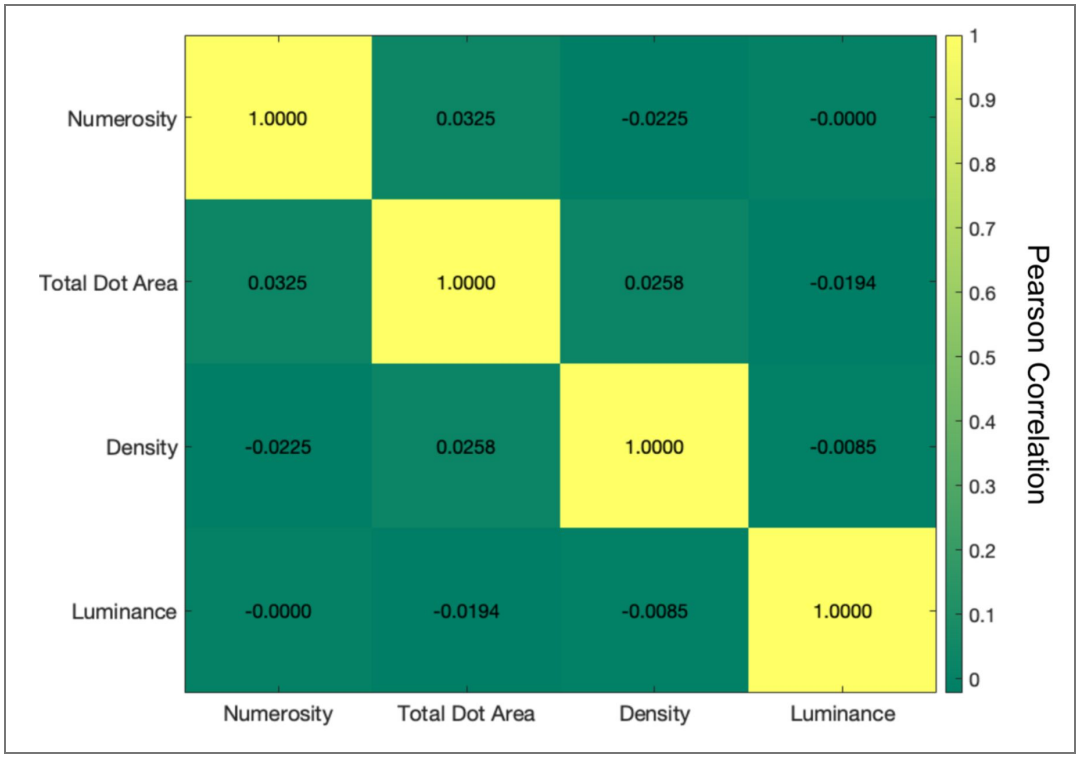
Statistical Inference

Cluster-based permutation testing was used to correct for multiple comparisons during statistical inference (Maris & Oostenveld, 2007). For all analyses,1000 permutations were employed with a cluster-forming alpha parameter of .05 and a significance threshold of .05. It is important to emphasize that cluster-based permutation testing does not provide precise information about when neural representations emerge. This limitation arises because cluster-level statistics are only defined for broader time windows that naturally encompass multiple individual time points (Sassenhagen & Draschkow, 2019).

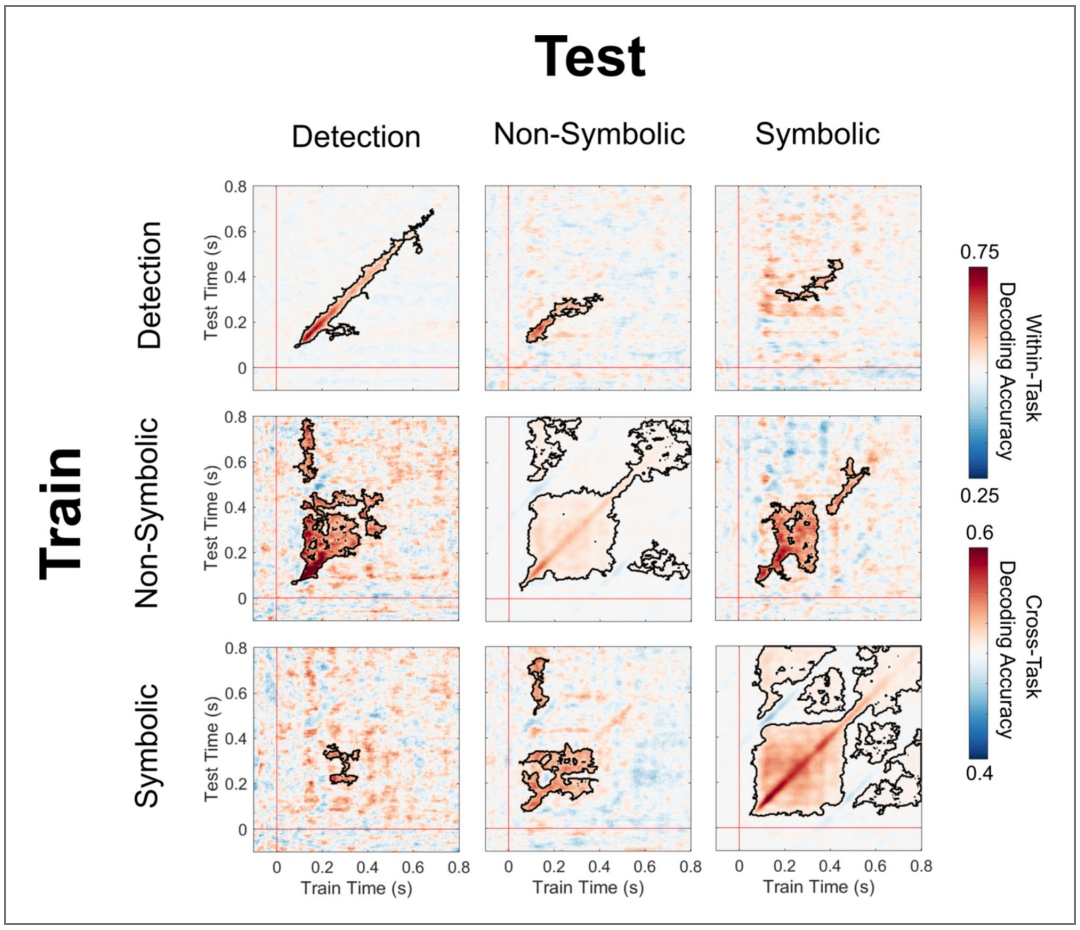
Bayes Factor Analyses

Cluster-based permutation tests are frequentist and as such cannot provide evidence for the null hypothesis (Dienes, 2011). In our case, this means that absence of significant (defined by frequentist permutation tests) cross-decoding between detection and numerical tasks cannot be interpreted as evidence for distinct representations of absence. To remedy this, we computed Bayes factors by applying Bayesian t-tests to decoding accuracy values across participants, using a Cauchy prior centred on zero with a scale parameter of 0.7071. For directional hypotheses, a halfCauchy prior was specified with a lower bound of 0.5. This lower bound was specified to allow for empirical decoding accuracies slightly above theoretical chance level (i.e. within an effect size of 0.5) to still provide evidence for the null. This is because decoding of neuroimaging data can often result in empirical chance levels that differ from theoretical chance (Stelzer et al., 2013; Teichmann, 2022). A lower bound of 0.5 was selected because multiple MEG decoding datasets have exhibited effect sizes up to 0.5 in baseline windows, where chance-level decoding is expected (Teichmann, 2022). Analyses were performed on the diagonal of the temporal generalisation matrices, resulting in a time-resolved vector of Bayes factors that could indicate evidence in support of either successful cross-decoding or an absence of crossdecoding. Our interpretation of Bayes factors follows standard thresholds (Jeffreys, 1961) which we log-transformed for visualisation and interpretability. Importantly, because Bayesian analyses are not related to overall error rates and are not used to threshold significance, they do not require correction for multiple comparisons (Teichmann, 2022).

Supplemental figures



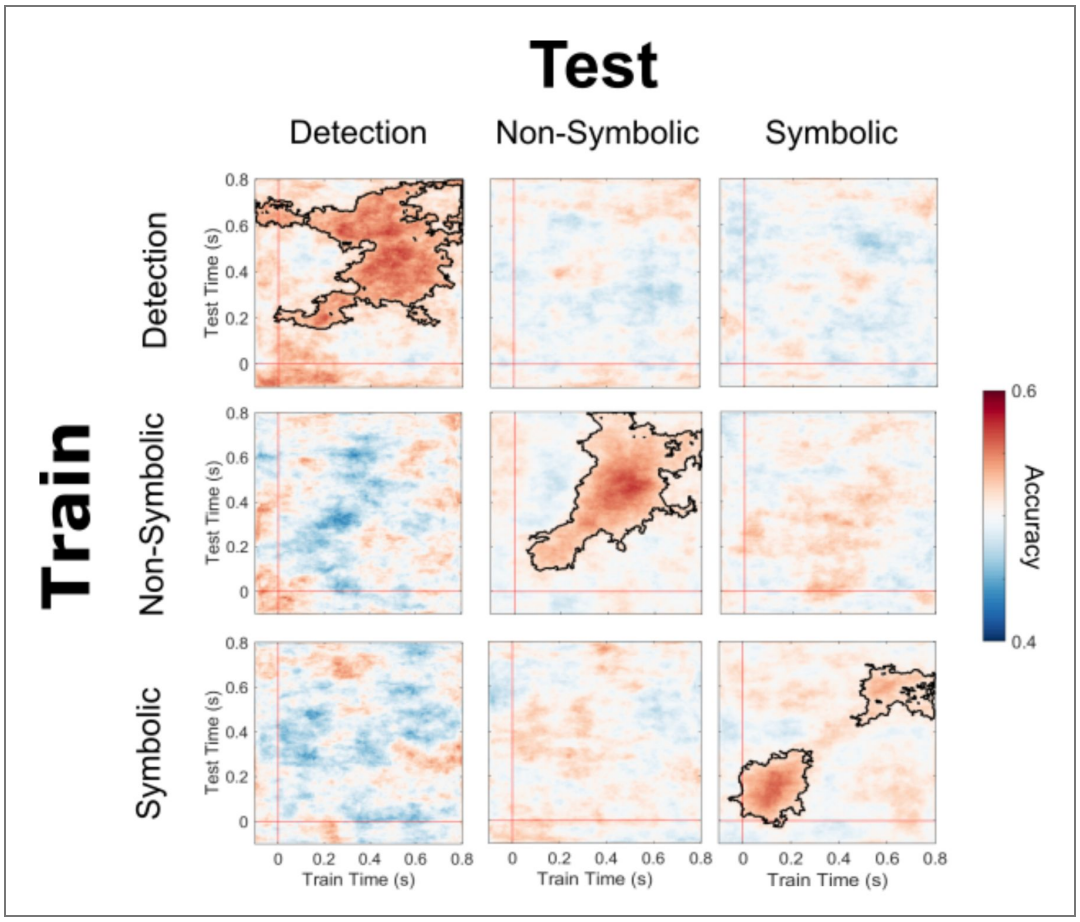
Supplemental Figure 1. Visual Features of Non-Symbolic Dot Stimuli Do Not Covary with Numerosity. Total dot area was measured as the number of pixels covered by all dots. Density was computed as the negative median Euclidean distance between dots, such that higher distances between dots results in lower density scores. Luminance was computed using Weber contrast. Values are Pearson correlation (r) coefficients.



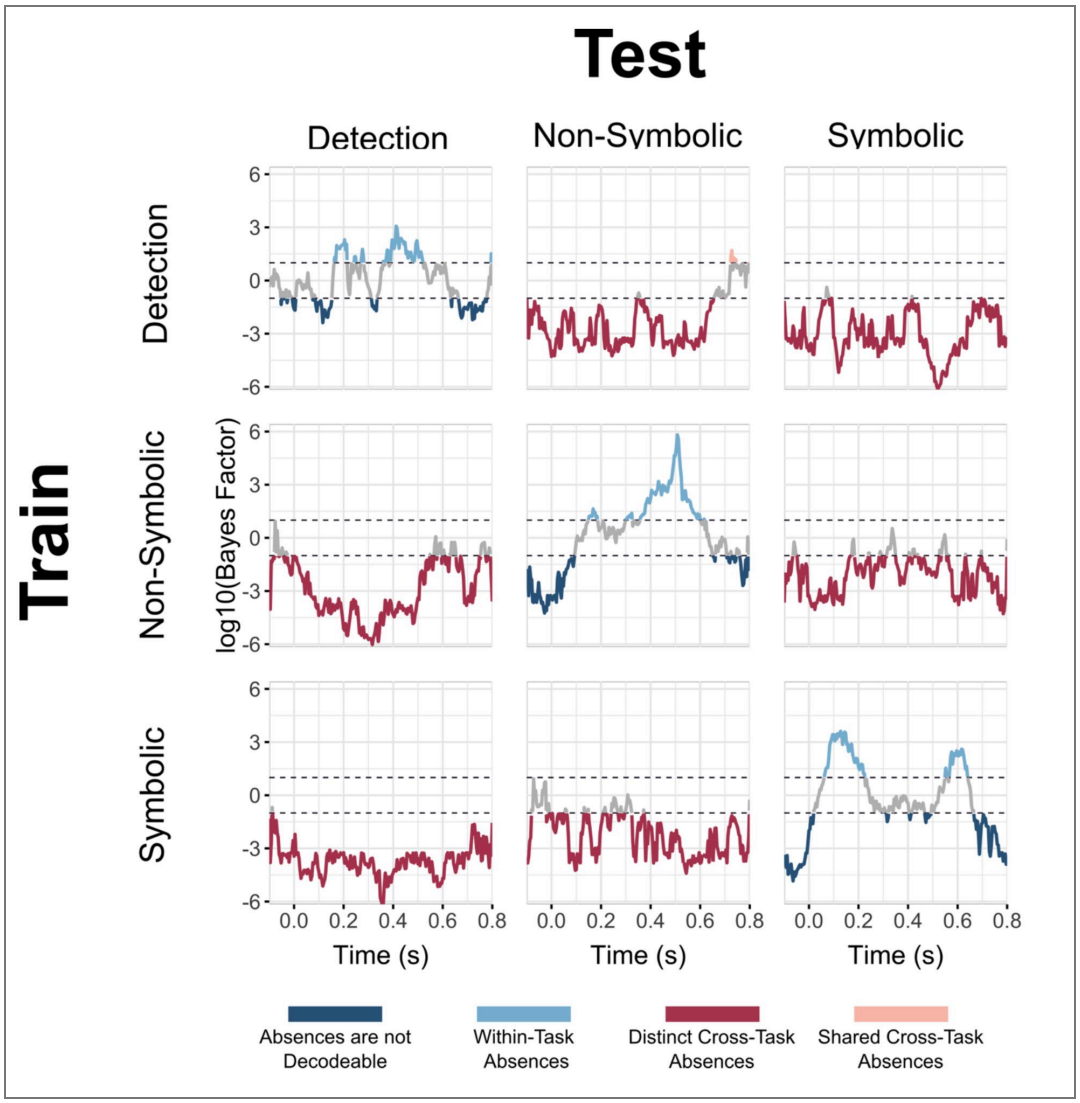
Supplemental Figure 2. Colour Can Be Decoded Within and Across All Tasks. *Diagonal*: WithinTask decoding of blue vs. orange stimuli was successful within all three tasks. *Off Diagonal*: Cross-Task decoding of blue vs. orange stimuli was successful across all pairwise combinations of tasks and traintest direction. Clusters represent areas of significant decoding as computed by cluster-based permutation tests.

Alpha Amplitudes Encode Domain-Specific Representations of Absence

Pre-stimulus neural activity in the alpha band is known to predict reports of stimulus presence and absence (Mathewson et al., 2009; Samaha et al., 2017). As such, it's possible that domain-general representations of absence may be encoded within the alpha frequency and decoding of broadband signals may lack the sensitivity to reveal them. To remedy this, we extracted the amplitude of participants' alpha rhythms over time and used this as input to decoding analyses. Training decoders to classify absence vs. presence and zero vs. non-zero within the detection and numerical tasks respectively was successful (Supplemental Figure 3, diagonal), indicating the existence of domain-specific representations of absence encoded within the amplitude of the alpha band. However, when these decoders were tested on alternative domains, no above-chance decoding was observed (all *p*s > .246; Supplemental Figure 3, off diagonal). Moreover, Bayes factors indicated strong evidence against domain-general representations of absence in the alpha band (Supplemental Figure 4). Interestingly, this result held even between the two numerical tasks, suggesting format-invariant representations of numerical zero (Figure 2) are not underpinned by fluctuations in alpha amplitude.



Supplemental Figure 3. Representation of Absence are Domain-Specific Within the Alpha Band. Decoding the amplitude of the alpha rhythms identified representations of absence within all three tasks, however none of these representations generalised across tasks. Clusters represent areas of significant decoding as computed by cluster-based permutation tests.



Supplemental Figure 4. Bayes Factors Show Strong Evidence for Domain-Specific Representations of Absence in the Alpha Band. Bayes factors computed for the diagonal of the temporal generalisation matrices in Supplemental Figure 3. There is strong evidence for domainspecific (and strong evidence against domain-general) representations of absence in the alpha band,

Data availability

MEG data has been deposited at *https://osf.io/xhqfc/* and all code for the analyses presented in this paper are openly accessible at at*https://github.com/benjybarnett/PerceptualNumericalAbsence*.

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Peer reviews

Reviewer #1 (Public review):

Summary:

The authors investigate whether the brain uses the same neural representations for "absence" when it comes to seeing nothing versus thinking of zero. To do this, they recorded MEG while participants performed two types of tasks: (1) a perceptual detection task where subjects reported the presence or absence of a faint visual stimulus, and (2) numerical comparison tasks where subjects saw streams of numbers or dot patterns (both including "0" or empty sets) and decided which of two color-coded streams had a larger average. Multivariate decoders were trained to distinguish "present" vs "absent" in the detection task and "zero" vs "non-zero" in the numerical tasks. As a sanity check, the authors first replicate that symbolic (digit "0") and non-symbolic (empty dot sets) zeros share a common neural code (cross-format generalization). Crucially, they find that this numerical "zero" code does not overlap with the code for perceptual absence: cross-decoding between the detection task and number tasks yields Bayes factors strongly favoring distinct representations. In other words, the brain's pattern for "no grating was seen" cannot decode the pattern for "the number zero was shown," and vice versa. A small brief cross-decoding effect around 300 ms was observed, which the authors attribute to low-level visual confounds (and which they test with an additional control decoder for stimulus presence), but overall the evidence supports a dissociation.

Strengths:

The authors investigate whether the brain uses the same neural representations for "absence" when it comes to seeing nothing versus thinking of zero. To do this, they recorded MEG while participants performed two types of tasks: (1) a perceptual detection task where subjects reported the presence or absence of a faint visual stimulus, and (2) numerical comparison tasks where subjects saw streams of numbers or dot patterns (both including "0" or empty sets) and decided which of two color-coded streams had a larger average. Multivariate decoders were trained to distinguish "present" vs "absent" in the detection task and "zero" vs "non-zero" in the numerical tasks. As a sanity check, the authors first replicate that symbolic (digit "0") and non-symbolic (empty dot sets) zeros share a common neural code (cross-format generalization). Crucially, they find that this numerical "zero" code does not overlap with the code for perceptual absence: cross-decoding between the detection task and number tasks yields Bayes factors strongly favoring distinct representations. In other words, the brain's pattern for "no grating was seen" cannot decode the pattern for "the number zero was shown," and vice versa. A small brief cross-decoding effect around 300 ms was observed, which the authors attribute to low-level visual confounds (and which they test with an additional control decoder for stimulus presence), but overall the evidence supports a dissociation.

Weaknesses:

My main concern is whether the perceptual and numerical tasks are truly matched aside from their "absence" content. The perceptual task is a simple yes/no detection of a faint grating, whereas the numerical tasks involve holding two streams of 5 items in working memory and comparing their average. These tasks differ in many ways (stimulus complexity, decision rule, cognitive load), so it is possible that the lack of cross-decoding is due to general task differences rather than a fundamental "absence vs zero" dissociation. The authors do partially address this by showing that other shared aspects (like color) can cross-generalize, but one might still worry that an "absence" decision in a detection task engages different attentional or decisional mechanisms than a "zero" decision in a numerical context.

The numerical averaging task closely resembles that used by Spitzer et al. (2017), who reported that both behavioral weighting and neural representational geometry exhibit anti-compression, with disproportionately stronger representations for larger numerosities. In contrast, the present manuscript interprets its decoding results as reflecting an ordered numerical continuum. It is therefore unclear whether the current analyses are sensitive only to ordinal structure or whether they also preserve the nonlinear representational geometry

reported previously. This distinction is important because the interpretation of zero as part of a numerical continuum depends on the geometry of that continuum. The authors should clarify whether their representational analyses are compatible with the anti-compressed neural number line described by Spitzer et al., or explain why the two studies yield different conclusions.

Spitzer, B., Waschke, L., & Summerfield, C. (2017). Selective overweighting of larger magnitudes during noisy numerical comparison. Nature Human Behaviour, 1(8), 145. *https://doi.org/10.1038/s41562-017-0145*

The authors attempt to account for non-numerical visual information by controlling for Total Dot Area and Density. While this is an important control, these two variables do not exhaust the visual dimensions that covary with numerosity in dot displays. A large body of work has demonstrated that multiple continuous features, including average item area, total surface area, convex hull (field area), and density, are inherently intercorrelated and cannot all be independently controlled simultaneously (e.g., Piazza et al., 2004; Gebuis & Reynvoet, 2004; Castaldi et al., 2019; Karami et al., 2025). Consequently, controlling only two features does not fully establish that the decoded signal specifically reflects numerosity. To better characterize the stimulus space, I encourage the authors to report the correlation matrix among the principal visual features of the dot arrays (average item area, total surface area, convex hull/field area, density, and numerosity). In addition, it would be informative to quantify the unique contribution of each feature to the neural data using a multiple-regression RSA or semi-partial correlations RSA, similar to the analyses employed by Castaldi et al. (2019) and more recently by Karami et al. (2025). Such analyses would provide a more rigorous assessment of whether the decoded representations uniquely reflect numerosity after accounting for correlated visual properties.

Piazza, M., Izard, V., Pinel, P., Bihan, D. L., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. Neuron, 44(3), 547-555. *https://doi.org/10.1016/j.neuron.2004.10.014*

Gebuis, T., & Reynvoet, B. (2011). The interplay between nonsymbolic number and its continuous visual properties. Journal of Experimental Psychology General, 141(4), 642-648. *https://doi.org/10.1037/a0026218*

Castaldi, E., Piazza, M., Dehaene, S., Vignaud, A., & Eger, E. (2019). Attentional amplification of neural codes for number independent of other quantities along the dorsal visual stream. eLife, 8. *https://doi.org/10.7554/elife.45160*

Karami, A., Castaldi, E., Eger, E., & Piazza, M. (2025). Distinct neural representational geometries of numerosity in early visual and association regions across visual streams. Communications Biology, 8(1), 1029. *https://doi.org/10.1038/s42003-025-08395-z*

The manuscript reports predominantly diagonal temporal generalization for non-symbolic numerosity, implying a rapidly evolving neural code. However, a recent study using time-resolved decoding of numerical representations (Karami et al., 2025) reported substantial off-diagonal temporal generalization, consistent with a temporally stable representational format. Although methodological differences between the studies may account for this discrepancy, the apparent contrast deserves discussion. In particular, it would be useful for the authors to clarify whether the differences arise from task demands, stimulus characteristics, preprocessing and decoding procedures, or from theoretical differences in what is being decoded. More generally, these findings raise the possibility that the temporal stability of numerical representations is task-dependent rather than fixed. If so, it would be interesting to discuss whether task demands might also influence the relationship between perceptual and conceptual representations of absence. Such a possibility could help explain

why cross-decoding was not observed in the present study and suggests an interesting direction for future research.

Karami, A., Castaldi, E., Eger, E., Hebart, M., & Piazza, M. (2025). Numerosity Is Directly Sensed and Dynamically Transformed in the Human Brain: Evidence from MEG-MRI Fusion. bioRxiv (Cold Spring Harbor Laboratory). *https://doi.org/10.1101/2025.11.15.687894*

Throughout the manuscript, the authors appear to treat non-symbolic numerosity as a conceptual representation and contrast it with perceptual absence. I find this interpretation insufficiently justified. A substantial body of behavioral (Anobile et al., 2013; Cicchini et al., 2016) and neuroimaging (Piazza et al., 2004; Castaldi et al., 2019; Karami et al., 2025) research has argued that non-symbolic numerosity is represented as a perceptual attribute extracted relatively early in the visual processing hierarchy, even if its precise computational origin remains debated. Consequently, it is not immediately clear why non-symbolic numerosity should be regarded as a conceptual representation comparable to symbolic number or the concept of zero. This distinction is important because it directly affects the interpretation of the negative cross-decoding results. If both perceptual absence and non-symbolic numerosity are primarily perceptual representations, the absence of cross-decoding cannot be taken as evidence that perceptual and conceptual absence are represented differently. Rather, it may simply indicate that these two perceptual representations encode different visual attributes. I therefore encourage the authors to clarify their theoretical position regarding the representational status of non-symbolic numerosity and to discuss how their interpretation relates to influential theories of numerical cognition that conceptualize non-symbolic numerosity as an early perceptual representation rather than an abstract conceptual one.

Anobile, G., Cicchini, G. M., & Burr, D. C. (2013). Separate mechanisms for perception of numerosity and density. Psychological Science, 25(1), 265-270. *https://doi.org/10.1177/0956797613501520*

Cicchini, G. M., Anobile, G., & Burr, D. C. (2016). Spontaneous perception of numerosity in humans. Nature Communications, 7(1), 12536. *https://doi.org/10.1038/ncomms12536*

Piazza, M., Izard, V., Pinel, P., Bihan, D. L., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. Neuron, 44(3), 547-555. *https://doi.org/10.1016/j.neuron.2004.10.014*

Castaldi, E., Piazza, M., Dehaene, S., Vignaud, A., & Eger, E. (2019). Attentional amplification of neural codes for number independent of other quantities along the dorsal visual stream. eLife, 8. *https://doi.org/10.7554/elife.45160*

Karami, A., Castaldi, E., Eger, E., Hebart, M., & Piazza, M. (2025). Numerosity Is Directly Sensed and Dynamically Transformed in the Human Brain: Evidence from MEG-MRI Fusion. bioRxiv (Cold Spring Harbor Laboratory). *https://doi.org/10.1101/2025.11.15.687894*

I have two related concerns regarding the discussion of Paul et al. (2022). First, I think it would be helpful to describe more explicitly what was measured in that study. To my understanding, Paul et al. quantified the aggregate Fourier power (AFP) of the stimuli. Moreover, AFP has primarily been discussed in the context of dot arrays with constant dot size within each stimulus. In the current manuscript, it is not entirely clear from the Methods whether dot sizes vary within displays. I therefore encourage the authors to explicitly describe how dot sizes were generated and varied across stimuli. If AFP is correlated with numerosity in the present stimulus set, it would also be helpful to explain how the analyses dissociate neural representations of numerosity from those potentially driven by AFP. Second, I am not entirely convinced by the argument that training a classifier to distinguish Hits from Correct Rejections is sensitive to aggregate Fourier power. It would be helpful if the authors could explain more explicitly why this decoding contrast should be expected to be

sensitive to AFP. As currently written, the logical connection between the AFP hypothesis and the proposed control analysis is not entirely clear.

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Reviewer #2 (Public review):

The authors tackle the question of whether conceptual absence is neurally encoded in the same way as perceptual absence. On one hand, the neural bases of perceptual absence have been largely investigated, as exemplified by the study of neural correlates of perception of aware vs. unaware stimuli, and on the other hand, the overlapping neural encoding of symbolic ('0') and non-symbolic (number of dots) formats of numerical absence has been previously established (Barnett & Fleming, 2024). However, the direct comparison of neural representations between numerical and perceptual absences remained to be investigated.

This article fills this gap by designing a Magneto-EncephaloGraphy (MEG) study using multi-voxel pattern analysis (MVPA) and temporal generalization to probe the similarity of neural patterns across the representation of perceptual absence (lack of stimuli), symbolic ('0'), and non-symbolic (number of dots) formats of numerical absence. They confirmed previously obtained evidence for shared neural representation across both formats of numerical absence. They report evidence for an absence of shared representation between both formats of numerical absence on one hand and perceptual absence on the other hand, while controlling for the confounding effect of low-level visual features. Their results overall support the conclusion that conceptual and perceptual absence are neurally encoded in a distinct way and speak in favour of a boundary between the representation of the concepts and the percept of absence.

Major strengths:

(1) Behavioral and neuroimaging results convincingly demonstrate that neural encoding of symbolic and non-symbolic absences is shared and situated on a graded, abstract neural number line, replicating previous results, notably from the authors themselves (Barnett & Fleming, 2024).

(2) They show that neural encoding of perceptual and numerical absence do not generalise across each other, while controlling for spurious confounds due to visual stimuli that are commonly shared in the cases of non-symbolic numerical absence and perceptual absences.

(3) They adequately use Bayesian analysis to distinguish absence of evidence vs. evidence of absence to support their claim.

(4) The interpretation of numerical absence as a representation of the concept of "nothingness" is adequate, although it might be further discussed by distinguishing the concept of "zero" on a number line from the concept of nothingness and that of an empty set (Nieder, 2016).

(5) The discussion about development and metacognition paves an interesting road for further investigation on the acquisition of the concept of zero, especially in light of debates on the progressive development of metacognitive abilities in children (Goupil & Kouider, 2019).

(6) Data and code are published with open-source access, allowing the community to further investigate the points as major weaknesses evoked below, if desired.

Major weaknesses:

(1) Interestingly, restricting the neural decoding method to the alpha band shows distinct representations across formats of numerical absence. This begs for providing more details on how neural representations of perceptual, symbolic, and non-symbolic absences differ at the source and frequency level and to report the decoding weights to better assess what drives the performance of the neural decoding algorithm in each case and whether they overlap with each other.

(2) Task-demands between perceptual (present vs absent) and numerical (lower vs higher) are different, raising concerns about whether these aspects of experimental design could drive, at least partially, the shared representational patterns across numerical representation of absence and their distinction from perceptual representation of absence.

(3) The same argument can also be raised for the way that the neural decoders of perceptual and numerical absences are trained and tested. Both formats of numerical absence are built using the same procedure (zero vs. rest) and differ from the way the decoder is built for perceptual absence (hits vs misses), which might possibly drive the difference observed here.

(4) It is thus unknown whether the claim supporting the evidence of absence holds as long as other counterfactual hypotheses that might drive these results are not excluded, such as the nature of the decoded features, the effect of task demands, or the way the neural decoder is trained, as mentioned above.

Overall, I was pleased by the quality of the methods and the clarity with which the question of the boundary between cognition and perception is addressed for the case of numerous and perceptual absence. While the methods used are well established in the field, the choice and rigor of their analysis and the controls provided stand as a convincing methodology to test their hypotheses, although they do not fully exclude alternative interpretations nor explore the wider extent of possibilities that may provide exhaustive evidence for showing that perceptual and numerical absences are distinctly encoded in the brain.

This work will be of great appeal to neuroscientists interested in comparing the representation of percepts and concepts across different formats, to psychologists interested in the origin of number representation, and to philosophers interested in debates on the boundary between cognition and perception.

Nieder, A. (2016). Representing something out of nothing: The dawning of zero. Trends in Cognitive Sciences, 20(11), 830-842.

Goupil, L., & Kouider, S. (2019). Developing a reflective mind: From core metacognition to explicit self-reflection. Current Directions in Psychological Science, 28(4), 403-408.

Barnett, B., & Fleming, S. M. (2024). Symbolic and non-symbolic representations of numerical zero in the human brain. Current Biology, 34(16), 3804-3811.

https://doi.org/10.7554/eLife.112088.1.sa0