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Review

Neural networks underlying magnitude perception: a specific meta-analysis of fMRI studies

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Daily life requires simultaneously processing spatial, temporal, and numerical inputs to form a valid mental representation of the environment. The interrelation between these perceptions has been a subject of theoretical debate. For instance, a theory of magnitude (ATOM) asserts that magnitude perceptions are processed in overlapping brain areas, which has been tested in behavioral and neuroimaging studies. We aimed to combine functional magnetic resonance imaging (fMRI) results using a coordinate-based meta-analysis to test this primary assumption of ATOM regarding overlapping brain areas. We conducted separate literature searches for space, time, and number perception following Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines. The analysis was based on 19 articles regarding space, 38 regarding time, and 31 regarding number perception. Coordinates were analyzed using the "Activation Likelihood Estimation" method, which focused on conjunction analysis. Double conjunction analyses revealed activations mainly in the fronto-parietal areas and insular cortex. The triple conjunction analysis revealed activations in the right hemisphere, specifically in the inferior parietal and inferior frontal areas (previously linked to magnitude perception) and the anterior insular cortex (implicated in interoception and salience). In support of the ATOM theory, these findings suggest that overlapping neural networks may underlie space, time, and number perceptions.

Keywords: activation likelihood estimation (ALE); number perception; space perception; time perception.

Introduction

Simultaneous perception of space, time, and numerosity is fundamental for streamlined perceptual experience and adaptive motor planning. These include everyday tasks of modern life, ranging from crossing the road, which involves judging distance, vehicle size, speed, and the crossing time, to office activities like precise clicking of a mouse to launch software. In more primal situations, quick assessment of threats in quantity, spatial positions, and approach speed, and finding the fastest path to safety, is often the key to surviving a threat. These scenarios necessitate rapid and integrated processing of spatial, temporal, and numerical information.

Developmental and comparative research have shown that time, space, and number perceptions aren't exclusive to adult human cognition. For instance, rhesus monkeys exhibit numerical magnitude representation between one and nine (Brannon and Terrace 1998). Ants, when displaced to make it impossible to follow a chemical trail, backtrack the spatial path they followed before being displaced, then continue movement in a search pattern. Rodents and pigeons cluster their responses around delays that predict reward (Gallistel 1989). Infants show heightened interest in novel or unexpected quantities of objects (Brannon and Roitman 2003). These and many other similar findings from comparative and developmental studies point toward an evolutionary well-preserved perception of space, time, and number. This is not surprising because integrating spatial, temporal, and numerical perceptions is crucial for the swift formation of mental representation and adaptive responses to stimuli (Hogendoorn 2022). The isolated processing of such vital information to be integrated later would exert more neural delay that could possibly make the difference between survival and elimination in a highly dynamic environment (Walsh 2003; Bueti and Walsh 2009; Hogendoorn 2022).

Many studies have demonstrated how time, space, and number perceptions are related, along with their interactions. The

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spatial–numerical association of response codes (SNARC) is the most prominent example showing the relation between space and number perceptions. It proposes a mental number line, where smaller numbers are represented on the left, while larger numbers are represented on the right in space (Dehaene et al. 1993; Nourouzi Mehlabani et al. 2020). This relationship is reflected in faster left-hand responses if the smaller numbers are presented on the left side, and vice versa, even when the primary task isn't focused on magnitude (Dehaene et al. 1993; Yan et al. 2021). A similar association between time and space is termed the spatial–temporal association of response codes (STEARC), which proposes a mental timeline that unfolds from left to right (Ishihara et al. 2008; Nourouzi Mehlabani et al. 2020). Accordingly, when stimuli of shorter duration are shown on the left visual space, participants had a faster reaction time (Casasanto and Boroditsky 2008; Ishihara et al. 2008). The comparable association between time and number perceptions is termed the temporal–numerical association of response codes (TiNARC). This relationship is manifested when two numbers are compared in terms of their respective durations displayed on a screen, resulting in the perception that the larger number stays on the screen for a longer period (Xuan et al. 2007; Fabbri et al. 2012). This effect can manifest with both symbolic and nonsymbolic numerosities (Xuan et al. 2007, 2009; Oliveri et al. 2008; Alards-Tomalin et al. 2016). That being said, these findings have been challenged by other studies that used equality judgments instead of "comparative judgments," which has been criticized to be bias-prone. These studies showed that larger stimuli are judged as shorter (Yates et al. 2012; see also Karşılar and Balcı 2019).

The interactions observed between spatial, temporal, and numerical perceptions by majority of the studies affirm the notion that these perceptions are processed together, at least partially. Several theories have been suggested to model possible interactions (Meck and Church 1983; Walsh 2003; Balci and Gallistel 2006; Casasanto et al. 2010; Hamamouche and Cordes 2019; Nourouzi Mehlabani et al. 2020). Among them, a theory of magnitude (ATOM) is one of the most prominent ones (Walsh 2003). According to the ATOM, perceptions of space, time, and number are processed as a metric for action through partially overlapping neural networks under the common framework of magnitude. Specifically, there should be a partially integrated neural network for all perceptual magnitudes (including luminosity), and neural networks of space, time, and number should overlap in terms of their magnitude properties. The foundation of this partial unity is based on the evolutionary notion that the data processed in the parietal cortex provide the necessary magnitude information for the accurate actions of organisms (Walsh 2003).

Most of the studies testing ATOM's predictions have focused on the reciprocal interaction between space, time, and number perceptions, the results of which have the notion of a common magnitude perception (DeLong 1981; Henik and Tzelgov 1982; Meck and Church 1983; Dehaene et al. 1993; Basso et al. 1996; Xuan et al. 2007; Szűcs and Soltész 2008; Bonato et al. 2012; Fabbri et al. 2012; Rammsayer and Verner 2015; Hamamouche and Cordes 2019; Nourouzi Mehlabani et al. 2020; Yan et al. 2021). In addition, various neurobiological evidence has been put forth to suggest that these perceptions may be processed together. To this end, brain imaging studies demonstrated activation in overlapping areas of the parietal lobe during tasks related to spatial, temporal, and numerical perception. On the causal front, when transcranial magnetic stimulation (TMS) was applied to the right parietal cortex, spatial, temporal, and numerical perception impairments were observed (Bueti and Walsh 2009). Additionally, animal single-neuron recording studies have shown that neurons previously defined as spatial neurons in spatial response maps can also encode temporal information (eg Leon and Shadlen 2003; Janssen and Shadlen 2005).

Based on the previous studies, Bueti and Walsh have further improved the ATOM by identifying the parietal cortex as the fundamental neurobiological locus of magnitude representations. They have also proposed that the right parietal cortex is not the sole cortical area related to magnitudes, suggesting that magnitude perception occurs within a magnitude system that also includes the left prefrontal cortex (Bueti and Walsh 2009). However, they did not provide a comprehensive model to explain the mechanism for the perception of magnitudes.

ATOM provides a compelling mechanism for the early processing of magnitudes, which is limited to the sensory processing of continuous magnitudes and their use for action (Walsh 2003). Thus, the effect extending to tasks such as mental arithmetic, mental rotation, spatial navigation, and beat perception are, while affected by basic interaction between magnitudes, not purely dependent on it. Explicit operations such as number manipulation and motor action selection are also proposed to rely on executive functions and linguistic processes. Not all aspects of magnitudes are suggested to have common processing, and magnitudes aren't necessarily computed together in higher levels of cognitive function (Bueti and Walsh 2009). In support of this, previous studies show that the influence of magnitude information on action doesn't extend to dynamic factors such as force, demonstrating the limits of magnitude information on higher-level processing (Fischer and Miller 2008).

ATOM, in its original form, suggested that magnitudes are mapped onto space, that there must be spatial-magnitude interactions, and the SNARC effects should extend to "Spatial–Quantity" interactions, namely SQUARC (spatial–quantity associations of response codes) effect (Walsh 2003; Bueti and Walsh 2009). SNARC-like effects have since been shown in many studies; however, there has been doubt cast on their validity for supporting ATOM. Some studies have proposed that SNARC-like effects are a result of the ordinality of given stimuli (Casasanto and Pitt 2019; Pitt and Casasanto 2022). Given that the SNARC effect occurs with many different numerical magnitudes based on the comparison between them, the ordinality effect could indeed be part of the reason. The studies propose that SNARC-like effects extend to noncontinuous ordinalities, such as days of the week or months of the year, and SNARC-like effects can be reversed based on culture, reading, and writing direction. Moreover, the preference for left-to-right ordering of number or size seems absent in uneducated people, suggesting there's no inherent left-to-right mapping of magnitudes (Pitt and Casasanto 2018, 2022; Pitt et al. 2021, 2023). While the proposal of magnitudes being partially integrated was derived from left–right space interactions, which could be more related to overlearned ordinalities, initial integration between number and space doesn't necessarily have to be directional. Numerical magnitudes affecting the grasping action and graspability judgment suggest that there must be integration on a more basic sensory level as well (Badets et al. 2007; Andres et al. 2008).

Beyond the reaction time tests, interactions between perceptual space–magnitude judgments were also studied. There's a large body of literature demonstrating the interactions between spatial and numerical magnitudes (Pinel et al. 2004; Hubbard et al. 2005; de Hevia and Spelke 2009; Cantlon 2012; de Hevia et al. 2012; van Dijck et al. 2012; Blini et al. 2013; Üstün et al. 2022). A study with number and space estimations shows spatial information

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interferes more with numerical judgment than vice versa (Dormal and Pesenti 2007). Numerous studies on space–time interactions showed space had a stronger effect on time perception (Casasanto and Boroditsky 2008; Xuan et al. 2009; Rammsayer and Verner 2014, 2016; Coull et al. 2015; Starr and Brannon 2016; Riemer et al. 2024), as well as showing symmetrical interactions (Cai and Connell 2015; Starr and Brannon 2016; Riemer et al. 2018; Vidaud-Laperrière et al. 2022). The direction of interaction between time and number also differs across studies. Some studies show a bidirectional effect between the two (Javadi and Aichelburg 2012; Arend et al. 2014; Togoli et al. 2021), while others show temporal magnitudes don't have a significant effect on number comparison (Roitman et al. 2007; Cappelletti et al. 2009; Xuan et al. 2009; Cappelleti et al. 2011). Asymmetry that's found in common tasks is attributed to language-related interference, working memory resources, and automaticity of processing in each magnitude dimension (Dormal and Pesenti 2013; Cai and Connell 2015; Starr and Brannon 2016).

Time being a bad disruptor for other tasks has been proposed before (Walsh 2003). This asymmetry could be due to time being an abstract dimension that is more subjective and affected more by mental state and cognitive load, thus making it more vulnerable to disruption (Hamamouche et al. 2018; Kondo et al. 2024). On the other hand, if both time and number are mapped onto space, they may influence each other through their interaction with space, converging at some point, which could suggest partial interaction between three magnitude dimensions. Magnitude dimensions may also purely be competing for working memory resources, but there's evidence to show otherwise (Serrien and Spapé 2021; Hallez and Balcı 2024; Sima and Sanayei 2024). One study attributed this asymmetry to number processing being more automatic than temporal processing, suggesting that when competing for the same neural resources, the more automatically processed dimension prevails (Roitman et al. 2007). A congruency study on time, space, and number found that temporal information affects the other dimensions weakly, while the spatial information has the strongest effect. Authors explained their results with the space being the most automatically processed dimension, followed by the number (Dormal and Pesenti 2013). Another study, however, attributed it to the time course in which number and time are processed: numbers are processed as soon as they are seen, while duration judgments can only be made after their disappearance. In this context, when a static numerical stimulus was given, an asymmetrical relation was observed, but when a temporal component was introduced to the spatial stimuli (number in this case), the duration–numerosity interaction became much more symmetrical (Togoli et al. 2021). This argument can be extended to the interaction of time with other magnitudes (space, luminance, etc.) and explain why time seems to be a bad disruptor and why interaction between magnitudes seems to be asymmetrical even on a perceptual level.

While in his original theory, Walsh (2003) proposed integration of continuous magnitudes onto space in the context of action, he also predicted multi-modal neurons in parietal areas that respond to space, time, and number at once and process them together. Based on this notion, ATOM is also interpreted as magnitudes having symmetrical interactions, as they would be coded on the same neural population (Walsh 2003; Casasanto and Boroditsky 2008; Bueti and Walsh 2009; Togoli et al. 2021). Thus, the evidence on asymmetrical interactions may seemingly disprove ATOM. However, this asymmetry could be specific to language-acquired humans. A study comparing the interference between spatial and temporal magnitudes in humans and monkeys has shown that rhesus monkeys show symmetrical interactions while adult humans show asymmetrical interactions (Merritt et al. 2010). Single-neuron studies on monkeys show the existence of multimodal neuron populations along with neurons responding to single magnitude dimensions (only space or only number, etc.), supporting the partial integration of magnitudes on a perceptual neural processing level (Colby et al. 1993; Leon and Shadlen 2003; Nieder and Miller 2004; Grefkes and Fink 2005; Nieder et al. 2006; Tudusciuc and Nieder 2007, 2009; Cook and Pack 2012; Roitman et al. 2012; Kraus et al. 2015).

The symmetry of interaction is difficult to show directly in infants. However, the processing of spatial, temporal, and numerical magnitudes was found to be related in several infant studies, some studies showing the same discrimination thresholds for magnitudes in general (Brannon et al. 2006; de Hevia and Spelke 2010; Srinivasan and Carey 2010; Walker et al. 2010; Lourenco and Longo 2011). While results are difficult to interpret, these relations would also support the notion that an intrinsic analog magnitude system exists in humans before linguistic development (VanMarle and Wynn 2006; Feigenson 2007). Moreover, an identical developmental trajectory of quantities (space, time, number, pitch, luminosity, etc.) in children was also suggested to support an analog magnitude system (Cantlon 2012).

Some studies in adults show that magnitude dimensions interact congruently only between dimensions of the same stimulus, in line with the view that magnitude(s) of the thing(s) is experienced by the integration of different dimensions of an object. A recent electroencephalogram (EEG) study showed that this interaction was likely to happen on a perceptual level (Togoli et al. 2022, 2025). In this context, the symmetrical interaction on a perceptual level may be present in humans, albeit influenced largely by cognitive processes, including language and judgment. Thus, overlearned reactions and associations may prevail in commonly used tasks, an effect similar to the ones seen in Stroop-like designs (Dormal and Pesenti 2012). More automatically processed magnitude dimensions may affect others more strongly, causing an observed asymmetry on most of the commonly used tasks (Merritt et al. 2010; Dormal and Pesenti 2013; Starr and Brannon 2016). The experience-dependent nature of conceptualizing higher cognitive functions, for example, emotions or good–bad mapping onto space, could possibly support this "overlearned concepts" notion (Pitt and Casasanto 2018). In a more basic action-based perspective, for example, judging the speed as the space an object crosses in time intuitively requires a more symmetrical interaction. Similarly, the movement priming based on the size and amount of stuff in space would occur more effectively with a more symmetrical interaction between numerosity and space (Badets et al. 2007; Andres et al. 2008). The effect of saccades on space, time, and number could also point to the close interaction between visuospatial magnitude perception and action (Burr et al. 2011).

Another prominent theory on magnitude perception agrees with the view that magnitudes (ordinalities, in its context) must be mapped onto space asymmetrically, albeit studying magnitudes on a different cognitive level. This theory shows evidence from linguistic metaphors, namely "conceptual metaphor theory (CMT)" (Lakoff and Johnson 1980; Casasanto and Boroditsky 2008). According to this view, the mapping onto space is evident in the way we speak about other magnitudes such as number (higher–lower, bigger–smaller), time (longer–shorter time, moving a meeting forward), and sound pitch (higher–lower sounds). Magnitudes in this context are ordinalities, and ordinalities are all mapped onto space, which is the dominant (and concrete) dimension. This view also extends the scope of concepts mapped onto space from

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physical dimensions to anything that has ordinal properties, such as months of the year, days of the week, alphabet, and emotional intensity (Casasanto and Boroditsky 2008). This is also a compelling theory that explains how the interactions of magnitudes extend beyond simple continuous dimensions and explains the emerging asymmetry between magnitudes when integrated into higher cognitive processes.

There's evidence of directional interactions between space and other magnitudes being dependent on culture and education (de Hevia and Spelke 2009; Shaki et al. 2012; Cooperrider et al. 2017; Pitt et al. 2021; Bulut et al. 2024; Dural et al. 2025), plastic, open to cueing and suggestion, and open to influence by recent experiences and even recent thoughts (Shaki and Fischer 2008; Fuhrman and Boroditsky 2010; Boroditsky et al. 2011; Casasanto and Bottini 2014; de la Fuente et al. 2014). For example, the most well-known of spatial–numerical associations, mental number line, has been shown to change direction based on one's writing direction; similarly, "past" and "present" are placed differently on the space based on the person's culture as well as recent thoughts (Shaki et al. 2012; de la Fuente et al. 2014). This supports spatial mappings being experience-dependent and plastic, which is in line with the notion that magnitudes are, in fact, ordinalities learned through interaction with the environment, mapped under the influence of experience (Casasanto and Boroditsky 2008; Pitt et al. 2023). The effect of learning and experience on judgment, however, doesn't refute the existence of interaction on the perceptual neural processing level. The symmetrical interactions reported in the literature would support this notion (Javadi and Aichelburg 2012; Arend et al. 2014; Cai and Connell 2015; Starr and Brannon 2016; Riemer et al. 2018; Togoli et al. 2021; Vidaud-Laperrière et al. 2022).

To validate any theory on cognition, defining the related brain areas is crucial. Much can be learned about the function of a brain area from the cognitive abilities lost when it is damaged. Most of the patient studies related to magnitude perception include neglect patients. Studies with right hemisphere damage, especially damage to the parietal and prefrontal cortex, provide evidence of both interaction and dissociation of magnitude processing. In a study with eight right brain damage patients with intact numerical arithmetic skills, spatial neglect was found to co-occur with number line neglect in the same direction (Zorzi et al. 2002). Conversely, a case study on a left brain damage patient with right extrapersonal spatial neglect and spatial memory deficit showed mental number line shift with left neglect characteristics due to a primacy effect and working memory deficits (van Dijck et al. 2011). Another study with 32 right brain damage patients showed double dissociation between spatial neglect and mental number line neglect, which is supported by other studies on neglect patients (Doricchi et al. 2005; Priftis et al. 2006a; Pia et al. 2012). This dissociation was explained by suggesting it may not mean number and space are distinct cognitive domains, and dissociation between visual and representational space was given as an example of such a phenomenon. Magnitude dimensions can be dissociated and still be part of a system that is partially integrated (Pia et al. 2012). Beyond number line neglect, studies have also demonstrated impaired temporal perception in neglect patients with right parietal cortex damage (Basso et al. 1996; Danckert et al. 2007; Merrifield et al. 2010; Calabria et al. 2011). Another study on a right spatial neglect patient suggested that right neglect is milder due to the absence of nonspatial deficits, showing the close interaction of spatial and temporal processing (Schneider et al. 2008). These studies show that temporal processing is also partially integrated with spatial perception.

Studies on neglect patients, however, should be treated with caution. It is obviously impossible to inflict the same amount of damage to the same brain area in humans, and no two brain damage patients have the same damage extent or depth. Since it is proposed that magnitude dimensions have partially integrated neural processing, damage to different brain areas could cause isolated disruption to each magnitude dimension if the damage affected an area specific to one magnitude dimension. The differences and dissociation of symptoms in neglect patients could also be related to the depth of the lesions. Indeed, studies show damage to the underlying white matter pathways is more detrimental to visuospatial processing compared to cortical damage to individual areas associated with this function, suggesting the depth of a lesion might be the biggest contributing factor to the severity, and maybe even occurrence of neglect symptoms (Doricchi et al. 2008; Pia et al. 2012).

In support of this, another study on anatomical correlates of neglect patients' symptoms found correlations between neglect type and severity and subcortical damage affecting white matter tracts (Aiello et al. 2012). The processing of a cognitive function being related to a single cortical area is an outdated view; connectivity and cooperation of brain areas are shown to be important in the processing of many cognitive functions (Mesulam 2012). As it stands, studying the connectivity between cortical areas related to magnitude processing may provide valuable clues about the inner workings of its neural basis, which is clearly shown by the abovementioned studies.

In real life, there's no explicit distinction between space, time, and numerosity. While they can be segregated in brain-damage patients or in a laboratory setting with meticulously designed experimental paradigms, they aren't *experienced* separately. For the most accurate evaluation of perceptual interaction, these magnitudes must be studied together on a neurobiological level. Neuroimaging is one of the most powerful tools for showing cortical involvement in function and gives valuable clues into the inner workings of the brain noninvasively. This information is valuable for figuring out if or how sensorimotor processing of magnitudes is related. There are a handful of neuroimaging studies that assess all three perceptions together (Skagerlund et al. 2016), and there is no study that has simultaneously evaluated spatial, temporal, and numerical perceptions in real-life situations, primarily due to the difficulties in constructing a suitable experimental paradigm. This makes it difficult to understand how magnitude perceptions work together and thus to test the basic principle of ATOM at the neural level.

Many studies evaluate time, space, and number perceptions in an isolated fashion using neuroimaging techniques. However, the reported brain activations can vary even with seemingly similar experimental procedures. This can be attributed to the fact that neuroimaging studies are subject to their own disadvantages. Usually relying on a smaller sample size, individual neuroimaging studies generally have a lower statistical power, which can lead to both Type I and Type II errors (Button et al. 2013). Neuroimaging studies also have many experimental procedures, paradigms, preprocessing methods, and analysis procedures, which can dramatically influence the results (Carp 2012). One of the most powerful approaches to combining these different sets of results without bias is meta-analysis (Müller et al. 2018). For this reason, a meta-analysis of neuroimaging studies carries value in capitalizing on and bringing clarity to the already reported.

Numerous meta-analyses to date have focused on time, space, and number in relation to sex differences, higher cognitive processes, or various diseases (Bowen et al. 2013; Kühn and

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Gallinat 2014; Alústiza et al. 2017; Faye et al. 2019; Lauer et al. 2019; Nazareth et al. 2019; Kasdan et al. 2022; Metcalfe et al. 2024). A smaller number of meta-analyses have also separately addressed space, number, and time perceptions of healthy participants without intervention within their respective literature (for space: Zacks 2008; Cona and Scarpazza 2019; for time: Nani et al. 2019; Teghil et al. 2019; for number: Arsalidou and Taylor 2011; Sokolowski et al. 2017; Yeo et al. 2017). Furthermore, several behavioral and neuroimaging meta-analyses have already demonstrated the cortical interactions between these perceptions (Wood et al. 2008; Hawes et al. 2019; von Sobbe et al. 2019; Cona et al. 2021, 2024). Of these, some of the most intriguing are by Cona et al. (2021, 2024). In 2021, Cona et al. published a meta-analysis of brain imaging studies on space and time perceptions. This study demonstrated that activations in brain regions related to these two perceptions occur along a gradient bilaterally on supplementary motor area (SMA), on the right parietal cortex, and on the right frontal cortex. Based on these findings, they concluded that the processing of spatial, temporal, and numerical perceptions occurs in partially overlapping neural networks, forming a gradient. They advanced the ATOM theory with a critical addition and proposed a new model, namely "*Gradi*ATOM" (Cona et al. 2021). In a follow-up study, which was the only meta-analysis study evaluating three perceptions together, Cona et al. (2024) added number perception to the previous meta-analysis and showed pairwise gradient maps between magnitudes, showing gradients in similar brain areas. They proposed that this result further supported their original gradient theory (Cona et al. 2021) and that the areas reflected functional overlaps related to magnitude. This was the first meta-analysis looking into the conjunction of all three perceptions together and working to deduce functional implications.

Although highly informative, coordinate-based neuroimaging meta-analysis has some limitations. Intuitively, it can be said that in coordinate-based neuroimaging meta-analysis, there seems to be a trade-off between noise and statistical power. To capitalize on most of the existing literature and also have a higher statistical power, researchers need to include a larger variety of tasks, which usually include different higher-level cognitive functions. In a coordinate-based meta-analysis, this can create a source of noise. Sticking to a limited variety of very similar tasks would lower the noise, but also means reaching fewer studies, which lowers the statistical power. Researchers have to accept one of these limitations.

Many earlier meta-analyses exploring interactions between space, time, and number have included higher-order cognitive functions (eg arithmetic tasks, mental rotation, navigation, and short-term memory) in their literature search (Hawes et al. 2019; von Sobbe et al. 2019). Cona et al. (2021, 2024) similarly included such tasks in their meta-analysis (see the keywords provided in both papers). However, Bueti and Walsh (2009) proposed that ATOM's strength lies in not having to extend to such functions and that the interactions between magnitude dimensions happen on a primarily perceptual level as an action-related magnitude system. In this context, while the gradients shown in *Gradi*ATOM studies may indeed reflect a functional convergence, it is hard to deduce the nature of the function. The function in question may or may not be magnitude perception per se in every area reported; some gradients might instead reflect higher order functions such as language, reasoning, planning, and memory. While the results of Skagerlund et al. (2016) can be compared for a possible confirmation and a better idea, of course, no single neuroimaging study is enough to confirm or refute the findings. The results require further confirmation through specifically designed individual neuroimaging and connectivity studies.

It is well-established that each of the three modalities discussed has its own distinct research areas. For instance, aspects such as navigation/location, distance, direction, and movement (Ekstrom and Hill 2023; Hiew et al. 2023; Kay et al. 2024). Similarly, numerical cognition ranges from basic abilities, like understanding discrete quantities and distinguishing between them, to more complex processes, such as performing arithmetic operations through symbolic representations (Faye et al. 2019). Like other cognitive systems, these modalities involve sensation, perception, thinking, imagery, memory, reasoning, and problem-solving. In this meta-analysis, we focused on these modalities specifically in relation to magnitude, which constrained the studies included accordingly. We excluded studies on the spatial domain that focused on navigation, shape, or movement-related components, such as mental rotation, mental imagery, or maze tasks. For instance, a meta-analysis investigating mental rotation revealed widespread activations across the occipital, temporal, parietal, frontal, and cerebellar regions (Tomasino and Gremese 2016). This extensive network reflects the high cognitive demands of mental rotation, which involves motor imagery and mental visualization rather than simple spatial magnitude processing. These findings suggest that mental rotation requires broader spatial skills, leading to widespread brain activity. For the numerical domain, we excluded studies that investigated the neural mechanisms underlying arithmetic operations because it has been demonstrated that different brain activations can occur even based solely on the type of operation (Arsalidou and Taylor 2011).

Similarly, for the time domain, we excluded studies emphasizing memory for longer time intervals. In general, we excluded tasks with a high cognitive demand or memory load. If the ATOM theory suggests that these perceptions share commonalities at the level of magnitudes, it is crucial to clearly define the boundaries to focus specifically on the aspects of these cognitive processes that relate to magnitude representations. Despite these boundaries, demonstrating any potential commonalities is essential for the theory's validity. However, there's a lack of meta-analyses that focus solely on perceptive tasks. Therefore, we prioritized contrasts derived from tasks that we believe specifically evoke neural responses related to magnitude. Focusing on these carefully selected tasks, we aimed to isolate the neural mechanisms underlying magnitude processing and avoid confounds from other (usually higher order) cognitive factors.

In our study, we used a coordinate-based meta-analysis of functional magnetic resonance imaging (fMRI) studies on space, number, and time perceptions, specifically choosing perceptual tasks in each magnitude dimension. In light of ATOM, we predicted that partially overlapping neural networks would be found for the three perceptions, the intersection of which might represent the magnitude system of the brain.

Materials and methods

Systematic review

We conducted three separate literature searches for time, space, and number perceptions. We aimed to gather one dataset for each perception and conduct conjunction and contrast analyses to identify common activation areas. For this, we followed "preferred reporting items for systematic reviews and meta-analyses (PRISMA)" flowcharts (Page et al. 2021a; Page et al. 2021b). We conducted literature searches on PubMed and Web of Knowledge databases using search codes containing chosen keywords,

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prepared in accordance with the algorithm of each database (Please see the keywords in Supplementary Material, Notes S1). Results were filtered by language (English), date (January 1, 2000 – December 31, 2022), and species (human) and then assessed independently by two researchers based on their titles and abstracts. Full texts of eligible studies were then taken into further evaluation.

Article selection processes were completed in accordance with our inclusion–exclusion criteria (Please see Supplementary Material, Supplementary Tables: Table S1 for the full list). Articles were required to have at least one contrast that fits all the inclusion criteria and have none of the exclusion criteria to be deemed eligible. We included magnitude-related fMRI studies that had 10 or more healthy adult participants, required motor response and active control conditions, and reported their results in a standard coordinate space. We excluded studies on patient groups, intervention studies, tasks involving higher-level cognitive processes, and multivariate or ROI analyses.

Regarding neuroimaging meta-analysis criteria, Müller et al. (2018) suggested that in a coordinate-based meta-analysis, the limitations of individual studies directly reflect on the results of the meta-analysis. Based on the criteria they put forward, we decided to exclude studies that had less than 10 participants since it would increase the risk of statistical error in initial time-series analyses. We also decided to include only one type of neuroimaging method in our analysis. Even though PET studies are commonly included in functional neuroimaging meta-analyses, the physiology underlying the test, the measurement, and the analysis techniques are notably different (Nickerson et al. 2001; Feng et al. 2004). As even small procedural changes in fMRI can cause differences in results, we opted to keep our studies limited to a single technique to keep discrepancies (and resulting possible statistical errors) to a minimum.

Our study was focused on the magnitude aspect of space, number, and time perception. Thus, we required fMRI paradigms to include magnitude-based tasks such as comparison, reproduction, or bisection tasks for each perception (see Altınok et al. 2022 method paper for a numerical comparison paradigm example). We excluded tasks involving higher level cognitive processes and tasks that are not directly related to the magnitude dimension, such as rhythm processing, mental arithmetic, and mental rotation, in order to show sensory aspects more clearly.

We included studies that used one perception task as a control for another. Although the mentioned magnitude domains are integrated according to the ATOM theory, they do not contain identical cognitive components. The existing studies reveal contrasts that differentiate these perceptions at their core, and the contrasts obtained relate to the brain regions associated with the investigated perception. For example, it has been shown that both nonsymbolic and symbolic number processes activate fronto-parietal networks, but they are processed through different pathways (Sokolowski et al. 2017). Our analysis aimed to demonstrate whether, by including these contrasts, there is indeed a neural intersection for these three percepts related to the ATOM theory and whether we can show this despite the differences.

After screening, the articles deemed eligible independently by two separate researchers were compared. In case of discordance between results, inclusion or exclusion of the article was decided by discussion and mutual agreement by researchers. Results from PubMed and Web of Knowledge databases were then combined, removing the duplicates, and foci from eligible contrasts were extracted. For time perception, we chose 570 foci taken from 39 studies, including 637 participants, of which 261 were female, 331 were male, and 45 participants' sex was not stated. For space perception, we chose 210 foci taken from 21 studies, including 390 participants, of which 160 were female, 203 were male, and 27 participants' sex was not stated. For number perception, we chose 380 foci taken from 33 studies, including a total of 655 participants, of which 303 were female, 334 were male, and 18 participants' sex was not stated. (Please see Supplementary Material, Supplementary Figures: Figs. S1, S2, and S3 for the PRISMA flowcharts of each literature search and Supplementary Tables: Tables S2, S3, and S4 for the full table of included articles).

Meta-analysis

For the meta-analysis, we used "activation likelihood estimation (ALE)" which is a coordinate-based neuroimaging meta-analysis method. Coordinate-based meta-analysis methods require only reported peak activation coordinates, which are almost always reported in the published articles. This allows a larger body of literature to be included in the analysis. While the meta-analysis results will carry the same disadvantages that the included articles have, with enough consideration for inclusion and exclusion criteria and a strong research question, the disadvantages can be kept to a minimum (Müller et al. 2018).

ALE is a voxel-based meta-analysis method developed by Turkeltaub et al. (2002) to combine coordinates reported in brain imaging studies in a way that can be validated statistically. ALE analysis runs all selected activation peak coordinates through a weighted quantitative analysis to combine and create a three-dimensional (3D) statistical image. A "null distribution" of the ALE statistic is also calculated based on the dataset. The combined image is then thresholded by the null distribution, which results in a 3D statistically significant activation likelihood map. ALE analysis can be run on GingerALE software developed in 2003 by the "Brain Map" group led by Peter T. Fox at the University of Texas and reported first in 2009 by Eickhoff and coworkers (Eickhoff et al. 2009, 2012; Turkeltaub et al. 2012). The revised version of the software runs on GingerALE version 3.0.2. (Turkeltaub et al. 2012). The software and the manual can be accessed through the "http://brainmap.org/ale/" website.

We created three separate datasets, one for each perception type, by combining the foci of chosen contrasts in eligible articles. All the foci in Talairach coordinates were converted to MNI coordinates with GingerALE, which uses the Lancaster transform (Lancaster et al. 2007; Laird et al. 2010). Datasets were created in MNI coordinates, and single dataset analyses were carried out to create a thresholded 3D statistical map for each perception. Each dataset included at least 21 experiments (in each of which at least 10 participants volunteered), which ensured that the results would have sufficient statistical power and were not driven by a single experiment (Eickhoff et al. 2016; Müller et al. 2018). Single dataset results were then run through conjunction and contrast analyses using default statistical parameters of cluster-level family-wise error threshold of $P < 0.05$ and 1,000 permutations with a cluster forming threshold of $P < 0.001$ (Eickhoff et al. 2016). The results were viewed in the "Multi-image Analysis GUI (Mango)" program that is a coordinate space viewer and four-dimensional (4D) image calculator.

GingerALE runs conjunction analyses by comparing correspondent voxels in each 3D image, comparing the ALE values, and assigning the lower ALE value to the voxel in the resulting image. This minimum value function uses thresholded meta-analysis images; thus, a second thresholding in the conjunction analysis isn't applied (Fox et al. 2013). However, it is not possible to run

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Table 1. Activation likelihood estimation meta-analytic results separately for space, time, and number perception.[a]

Cluster size (mm3)	Brain area (label of closest gray matter voxel within ± 5 mm)	BA	Max ALE value	MNI coordinates		
				x	y	z
1. Space perception: 210 foci, 21 experiments, 390 subjects						
2376	Right parietal lobe supramarginal gyrus	40	0.0224	42	−38	42
	Right inferior parietal lobule	40	0.0156	42	−50	54
2248	Left inferior parietal lobule	40	0.0277	−34	−48	50
	Left inferior parietal lobule	40	0.0210	−38	−40	46
1816	Right parietal lobe, precuneus	7	0.0283	18	−64	56
1384	Right inferior frontal gyrus	9	0.0190	52	14	28
1096	Left inferior temporal gyrus	37	0.0211	−46	−66	20
1088	Right middle occipital gyrus	19	0.0186	38	−78	24
912	Right middle frontal gyrus	6	0.0164	28	−2	48
	Right middle frontal gyrus	6	0.0143	30	−2	58
784	Right cerebrum sub-lobar insula	13	0.0167	34	24	4
2. Time perception: 570 foci, 39 experiments, 637 subjects						
7144	Right inferior frontal gyrus	9	0.0330	52	12	24
	Right inferior frontal gyrus	44	0.0308	52	16	12
	Right sub-lobar insula	13	0.0280	50	16	0
	Right sub-lobar insula	13	0.0262	36	22	0
6984	Left sub-lobar claustrum	-	0.0421	−32	22	−2
	Left sub-lobar lentiform nucleus, putamen	-	0.0297	−14	8	0
	Left sub-lobar insula	13	0.0247	−48	16	−6
	Left inferior frontal gyrus	44	0.0203	−52	10	14
	Left sub-lobar insula	13	0.0197	−50	14	2
6232	Right medial frontal gyrus	6	0.0443	6	18	46
	Right superior frontal gyrus	6	0.0323	4	10	52
3128	Right sub-lobar caudate body	-	0.0379	12	8	2
1664	Right inferior parietal lobule	40	0.0296	44	−38	44
	Right inferior parietal lobule	40	0.0186	56	−36	44
3. Number perception: 380 foci, 21 experiments, 655 subjects						
7784	Right inferior parietal lobule	40	0.0435	50	−34	50
	Right inferior parietal lobule	40	0.0397	44	−44	50
	Right superior parietal lobule	7	0.0227	32	−56	44
	Right parietal lobe, precuneus	7	0.0208	24	−66	40
	Right parietal lobe, precuneus	7	0.0166	22	−70	50
2720	Right frontal lobe, precentral gyrus	6	0.0403	48	6	26
1800	Right cingulate gyrus	32	0.0259	8	30	36
	Right superior frontal gyrus	8	0.0220	8	22	52
1664	Insula	13	0.0363	34	22	0
1512	Left inferior parietal lobule	40	0.0209	−32	−48	48
	Left supramarginal gyrus	40	0.0196	−40	−40	42
	Left inferior parietal lobule	40	0.0174	−48	−36	50

[a]Cluster level inference $P < 0.05$ Family-wise Error correction (FWE).

a triple conjunction analysis in GingerALE software. For the conjunction of space, time, and number perceptions, we used the same minimum value function in the Mango "Image Calculator" tool to create the triple conjunction 3D map using the same principles as in GingerALE.

Results

Separate meta-analysis results for space, time, and number perceptions

The size, peak coordinates, and maximum ALE values of the voxel clusters that show significant activation probability for space, time, and number perceptions are given in Table 1. The largest cluster seen in the space perception meta-analysis was in the right parietal lobe, in the intraparietal sulcus (IPS) area, and the second largest cluster was in the left parietal lobe. Other significant activation likelihood clusters were observed in the right precuneus, right inferior and middle frontal gyri, right middle occipital gyrus, right insula, and left inferior temporal gyrus.

A large portion of the significant activation likelihood areas were observed in bilateral basal nuclei for time perception, located predominantly on left hemisphere basal nuclei. Other significant activation likelihoods were observed in the right superior, medial and inferior frontal gyri, right inferior parietal lobule around the IPS and right insula.

The main significant activation likelihood clusters seen for number perception were observed bilaterally at the IPS. Right parietal lobe activations were significantly larger compared to left. Activations were also observed in the right precentral gyrus, right superior frontal gyrus and right cingulate gyrus.

Conjunction analyses

Conjunction analysis for space and number perceptions yielded results mainly located bilaterally in the IPS. Significant activation likelihoods were also observed in the right inferior frontal gyrus and right insula. The conjunction of space and time perception yielded results in similar areas on the right hemisphere only. Results of time and number perceptions conjunction analysis

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Table 2. Conjunction meta-analysis results.

Cluster size (mm3)	Brain area (label of closest gray matter voxel within ± 5 mm)	BA	Maximum ALE value	MNI coordinates		
				x	y	z
1—Space and number perception conjunction						
1016	Right inferior parietal lobule	40	0.0210	40	−40	44
	Right inferior parietal lobule	40	0.0148	40	−48	54
936	Right inferior frontal gyrus	9	0.0183	52	12	26
880	Left inferior parietal lobule	40	0.0209	−32	−48	48
	Left inferior parietal lobule	40	0.0178	−40	−40	44
512	Right sub-lobar insula	13	0.0167	34	24	4
2—Space and time perception conjunction						
856	Right parietal lobe, supramarginal gyrus	40	0.0224	42	−38	42
744	Right inferior frontal gyrus	9	0.0190	52	14	28
480	Right sub-lobar insula	13	0.0167	34	24	4
3—Time and number perception conjunction						
1408	Right inferior frontal gyrus	9	0.0269	50	10	26
1352	Right sub-lobar insula	13	0.0262	36	22	0
1064	Right inferior parietal lobule	40	0.0250	44	−40	48
680	Right superior frontal gyrus	6	0.0209	8	22	50
	Right medial frontal gyrus	6	0.0152	8	26	42

showed significant activation likelihood areas in similar areas with the addition of superior and medial frontal gyri, all clusters in the right hemisphere (Table 2, Fig. 1).

Triple conjunction analysis for space, time, and number, run in the Mango image calculator showed three significant activation likelihood clusters in the right hemisphere: inferior frontal gyrus, inferior parietal lobule, and anterior insula (Table 3, Fig. 2).

Discussion

In the present study, we evaluated the fMRI studies on space, number, and time perceptions by a coordinate-based meta-analysis. We analyzed double conjunctions and the triple conjunction between these three perceptions. We were especially interested in the triple conjunction between space, time, and number which we propose to represent neural networks for the magnitude system of the brain. We will only discuss the conjunction results within the scope of this article, considering the large number of results obtained from the meta-analysis for the three perceptions separately.

As we discussed in the introduction, meta-analysis studies have some limitations. One of them is the number of participant's cutoff chosen in the inclusion criteria. We chose to include studies with 10 or more participants. One might think if there was a study with less than 10 participants reporting results that would disagree with our findings and if we included it in the analysis, our results could be different. There were indeed studies we excluded only because of the participant numbers. Scanning their results, we found that their results were similar to our findings (Eger et al. 2003; Ansari and Dhital 2006).

Conjunction analyses

Our results have shown inferior parietal lobule (IPL), inferior frontal junction (IFJ), SMA, and insula activations across time–space, time–number, and space–number conjunctions. Previous neuroimaging meta-analyses of the conjunction of perceptions have shown similarities as well as differences. The method of coordinate-based meta-analysis is the same in the studies, which suggests any differences must be the result of selected studies. We discussed the similarities under the appropriate brain areas, but the different activation findings below.

A previous meta-analysis on symbolic number perception, mental rotation, and arithmetic suggested that mental rotation and number conjunction should show brain areas related to magnitude judgments and spatial–numerical mappings. The areas they have shown for this conjunction are bilateral superior and inferior parietal lobe activations, and left precuneus; they didn't show insular activations (Hawes et al. 2019). Bilateral precuneus activation has also been noted in a more recent meta-analysis with a larger number and variety of tasks included, suggesting this could indeed be an important area for space and time conjunctions (Cona et al. 2024). A previous fMRI study adds supporting evidence for the functions of precuneus for space–number interactions, showing bilateral precuneus activations for the number line estimation task (Vogel et al. 2013).

Precuneus is a core brain area in default mode network (DMN) and has been implicated in visuospatial navigation and mental rotation, as well as SNARC effect and symbolic number comparison (Ohnishi et al. 2006; Fransson and Marrelec 2008; Krause et al. 2014; Mahayana et al. 2014; Utevsky et al. 2014; Brodt et al. 2016; Dordevic et al. 2022; Duan et al. 2025). Navigation and mental rotation require higher-level cognitive processes, and the symbolic number system includes language function. SNARC effect has mostly been tested on symbolic number comparison, mental number line, or parity judgments, which can also include linguistic processes. In this context, the left precuneus activations might be related to higher-level mental processes rather than magnitude-related perceptual processing. On the other hand, right precuneus activation has been found in a brightness estimation task, which Bueti and Walsh (2009) previously defined as a perceptual magnitude (Vogel et al. 2013). It is notable that while right precuneus activations have been reported in the space and number literature, our study hasn't shown activations in this area. This could be due to the lower number of studies we included; further studies on this specific subject would bring more clarity to the functions of precuneus in magnitude perception.

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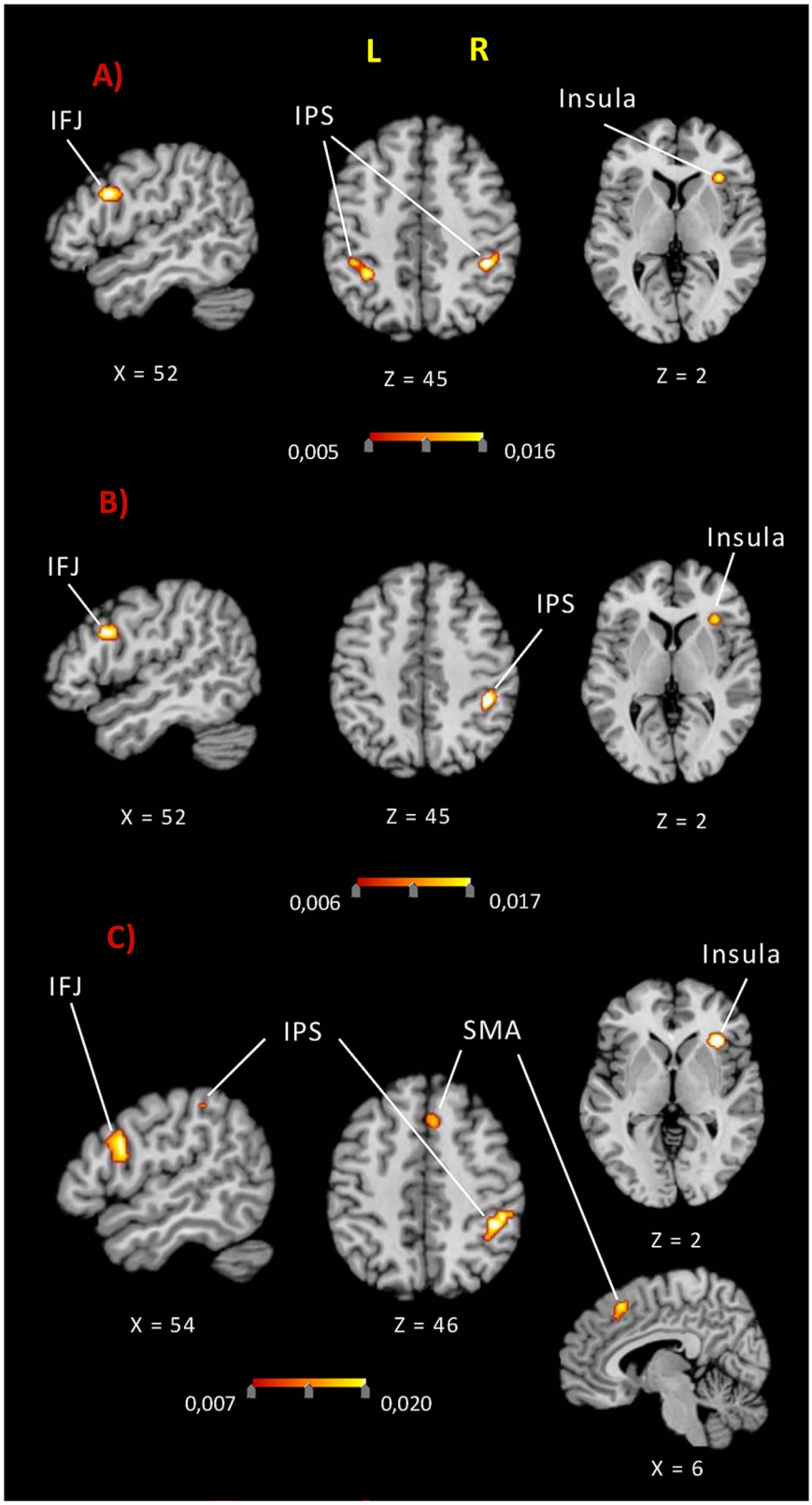


Fig. 1. Conjunction analysis results showing brain regions that exhibit common ALE activations for: (A) space and number, (B) space and time, and (C) number and time. The results are displayed on 2D sections, including sagittal (x), coronal (y), and axial (z) planes, with activations shown in color representing z-scores above the threshold. Colors indicate the ALE values for each voxel, with yellow representing the most significant ALE values. IFJ, inferior frontal junction. IPS, intraparietal sulcus. SMA, supplementary motor area.

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Table 3. Triple conjunction meta-analysis results.

Cluster size (mm3)	Brain area (label of closest gray matter voxel within ± 5 mm)	BA	Maximum ALE value	MNI coordinates		
				x	y	z
700	Right inferior frontal gyrus	9	0,0183	52	12	26
672	Right inferior parietal lobule	40	0,0204	42	−40	44
507	Right sub-lobar insula	13	0,0167	34	24	4

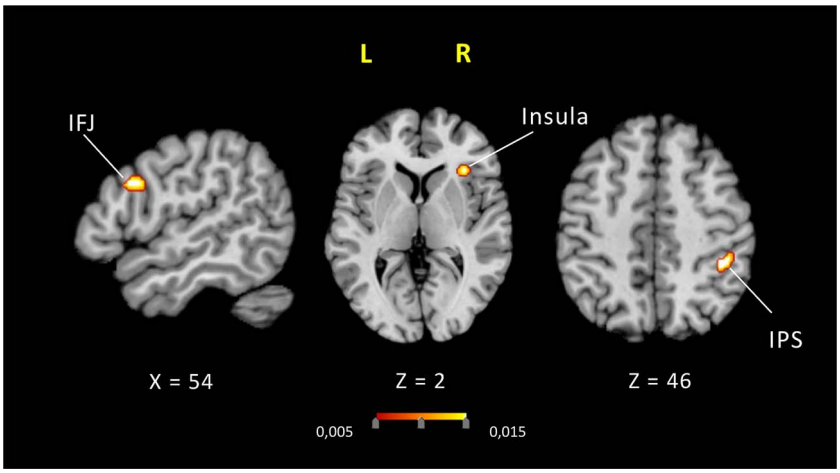


Fig. 2. Results from the conjunction analysis of space, time, and number are depicted on 2D sagittal and axial sections. Activations are color-coded to reflect z-scores exceeding the threshold, with colors representing ALE values for each voxel (yellow highlights the regions with the highest ALE values). The analysis reveals a lateralized pattern toward the right hemisphere for the common activations across the three modalities. IFJ, inferior frontal junction. IPS, intraparietal sulcus.

Another conjunction meta-analysis focused on the retrieval of spatial and temporal episodic memory has found completely separate brain areas, suggesting that beyond the initial processing, the networks for space and time might not be even partially overlapping (Torres-Morales and Cansino 2024). This is an interesting finding, considering magnitude processing is found to be related on both perceptual and executive levels, including language and overlearned concepts (see: Introduction). A more perceptually focused meta-analysis on space and time showed activations in similar areas to our space–time conjunction analysis, except they showed left hemisphere activations and SMA activations as well (Cona et al. 2021). We discussed our conjunction analysis findings under brain area headings; thus even though we didn't find time–space interactions in SMA, we will discuss it in more detail below.

Inferior parietal lobule (IPL)

In the conjunction analyses we ran, one of the most notable brain areas activated was the IPL. This is an area that has a dominant role in spatial perception and attention (Zacks 2008; Cicek et al. 2009; Sarwar and Emmady 2023). A previous meta-analysis also supports the importance of IPL in spatial perception, showing bilateral activations in IPL regions (Cona and Scarpazza 2019). This area has also been implicated in the neural basis of time perception, and possibly in directing attention to time (Basso et al. 1996; Rubia and Smith 2004). Animal studies have shown the existence of neurons coding temporal information in this cortical area (Leon and Shadlen 2003; Janssen and Shadlen 2005). In an exhaustive meta-analysis on time perception, Nani et al. (2019) have shown activations for subsecond motor and suprasecond perceptual tasks, suggesting IPL might have different roles in different subprocesses of time perception. Another meta-analysis on internally-based and externally-cued time perception tasks showed bilateral IPL activation in internally-based timing tasks (Teghil et al. 2019). Similarly, the inferior parietal cortex also holds a significant place in Dehaene et al.'s triple code model and is suggested as a domain-specific brain area for the perception of number (Dehaene et al. 2003; Üstün et al. 2021). This theory is supported by meta-analyses on numerical processing and calculations, where robust activations in bilateral IPL for both symbolic and nonsymbolic perceptual tasks and arithmetic tasks are shown (Arsalidou and Taylor 2011; Sokolowski et al. 2017; Yeo et al. 2017). In humans, it is believed that there may be number neurons tuned to specific numerosities in the IPS (Nieder 2016; Clarke and Beck 2021).

TMS can also give more clues on this subject since it can stimulate or inhibit a brain area selectively, so the functional changes can be kept consistent across participants (Walsh and Cowey 2000). Studies applying inhibitory rTMS (repetitive TMS) over IPS found that both left and right IPS inhibition affected symbolic and nonsymbolic number perception (Cappelletti et al. 2007, 2009). Right IPS disruption caused impaired automatic magnitude processing (Cohen Kadosh et al. 2007); but one study found facilitation of numerical reaction times with right IPS disruption with TMS, and they proposed that while continuous numerical magnitude processing may happen in right IPS, the connections may be inhibitory (Cappelletti et al. 2007). Left IPS disruption was found to cause impaired symbolic number processing (Sandrini et al. 2004). These results support the notion that both hemispheres are involved in numerical processing, where left IPS is more related to the linguistic integration of numerosity, such as number symbols, while right IPS mainly processes magnitude

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information. TMS studies on space also show the importance of the parietal cortex in spatial processing. Studies reported that when posterior parietal cortex function is disturbed, participants show neglect-like bias on a line bisection task (Bjoertomt et al. 2002; Oliveri and Vallar 2009; Salatino et al. 2019). Another study found both the right and left inferior parietal lobes are important in the maintenance of spatial attention, but not in object features (Lee et al. 2013). Time perception was also disrupted when TMS was applied to the parietal cortex: disruption of IPS function diminished numbers' effect on time perception and time estimation accuracy (Alexander et al. 2005; Hayashi et al. 2013a; Hayashi et al. 2013b). These studies show the critical role of the parietal cortex in magnitude processing. As it stands, it is intuitive to assume that an interaction between perceptions may occur in this cortical area.

The parietal cortex has been suggested as one of the important cortical areas for magnitude interactions (Bueti and Walsh 2009; Cappelletti et al. 2011; Hayashi et al. 2013a; Riemer et al. 2016; Üstün et al. 2022). Studies have also shown support for interactions between perceptions in this area. Patients with left neglect syndrome can show disturbances in perception of number and time, which supports the notion that the right parietal cortex, along with the underlying white matter connections to the frontal areas, holds an important role in the interaction between space and time perceptions (Basso et al. 1996; Zorzi et al. 2002, 2012; Priftis et al. 2006b; Danckert et al. 2007; Pia et al. 2012). Monkey homolog of parietal lobe areas is also where most magnitude-responsive neurons were reported, which makes this area one of the most likely for perceptual integration of magnitude dimensions (Leon and Shadlen 2003; Nieder and Miller 2004; Tudusciuc and Nieder 2007, 2009; Kraus et al. 2015).

Inferior frontal junction (IFJ)

An important area we found in the conjunction analyses was located in the posterior of the inferior frontal lobe, around an area that can be commonly referred to as BA 6, 9, or 44. This area has been defined as the IFJ (Derrfuss et al. 2004, 2009; Brass et al. 2005). The possible Talairach coordinates for this junction have been defined as x coordinate between +/−30 and +/−47, y coordinate between −1 and 10, and z coordinate between 27 and 40. However, it should be noted that these aren't absolute coordinate limits for the area, and the anatomical variances between participants around this area and possible errors during the smoothing of images should be considered when interpreting functional neuroimaging results (Derrfuss et al. 2004, 2009). Using linear transformation given in GingerALE software, an approximate coordinate limit in MNI space would be x coordinate between −31 and −49 for left IFJ and between 33 and 51 in right IFJ; y coordinate between 1 and 13; z coordinate between 24 and 39 (Lancaster et al. 2007; Laird et al. 2010). While the activation peaks in our double conjunction results aren't perfectly within these limits, the localization of the activation is consistent with the general location of IFJ.

IFJ has been suggested to have a critical role in cognitive control, especially in task switching and working memory updating. It is thought that, being in the middle of prominent cortical areas, IFJ is in a strategic location for the integration of information. Studies have shown left or bilateral IFJ activations in tasks where subjects need to update task rules or working memory (Roth and Courtney 2007; Derrfuss et al. 2009). It is worth noting that in our study, we found activations in the right IFJ (rIFJ) alone.

Studies on the rIFJ or the lateralization of function in IFJ are relatively few. Zanto et al. (2010) found that distinct subregions of IFJ were important in top-down modulation of color and motion visual association cortex areas (Zanto et al. 2010). Later in a TMS study, they found that impaired rIFJ function negatively affected the attention to color, but not motion, also indicating that top-down control directly affected the working memory performance (Zanto et al. 2011). Another more recent study found increased connectivity between rIFJ and V4 for feature attention and associated it with increased performance in behavioral analysis. They argued their findings to be in support of rIFJ playing a significant role in preparatory control of feature attention (Meyyappan et al. 2021). It is interesting, to say the least, to see a right lateralized IFJ activation in a meta-analysis of studies with active control conditions, which required the participants to attend to features of the control stimulus as well. This suggests that rIFJ is activated more strongly during magnitude-related tasks. TMS over the right inferior frontal lobe has been shown to affect categorical duration discrimination (Hayashi et al. 2013a). Another study showed disruption of task-related (explicit) number–space interactions with TMS over right IFG areas, but no disruption in task-irrelevant (implicit) conditions (Rusconi et al. 2011). Mental number line bisection tasks (with numbers presented orally) were shown to be disturbed when right frontal cortical or subcortical areas are damaged (Doricchi et al. 2005). These studies would suggest that the right inferior frontal cortex, especially IFJ, where we found converging activations in our study, might have a more specific role than feature attention, possibly a role in integrating magnitude information to be used in higher-level cognitive functions.

Supplementary motor area (SMA)

Adjacent to the right IFJ cluster, for time and number perception conjunction meta-analysis alone, another smaller cluster in the superior and medial frontal gyrus was observed. This area is consistent with Brodmann's area 6 (BA 6), closer to the SMA. For spatial perception, the activation in this area has previously been shown to be related to the type of stimulus and chosen experimental design (Tomasino and Gremese 2016). This area is an important part of fronto-striatal pathways and has been strongly implicated in the motor response and timing of movement (Schubotz et al. 2000; Rubia and Smith 2004). In an in-depth meta-analysis of temporal processing neuroimaging studies, it was shown to be a robust activation area across experimental design types and further reliability analyses (Nani et al. 2019). SMA and Pre-SMA have also been implicated in ordinal representations of task-related responses or ordinal categorization of certain items (Nieder and Dehaene 2009).

While SMA activation was seen in our meta-analyses for all three perceptions, in our conjunction analyses, notably, only time and number conjunction showed activation in this area. Visually evaluating the results in Mango, we noted that while in all individual perception meta-analysis results there were significant SMA activities in nearby regions, double conjunctions reveal no overlap except for time and number conjunction. This could mean that certain subregions of SMA do specific neural computations for each modality. However, a previous meta-analysis on time and space perceptions found a strong overlap in the area and suggested it to have functional implications for the co-processing of time and space perception (Cona et al. 2021). This difference between our results could be due to the different inclusion–exclusion criteria, which resulted in a difference in the studies included in the analysis. Our study included only fMRI studies and only magnitude-oriented tasks, which may explain the difference in results. Our strict criteria, however, also means we included

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a significantly lower number of studies in comparison, and this may have resulted in a lower statistical power possibly causing a false negative in our conjunction analyses. This possibility is supported by the significant activation found in right SMA in the triple conjunction analysis in a previous fMRI study (Skagerlund et al. 2016).

The activation found in time–number conjunction analysis could be due to motor responses being required for both perceptions. On the other hand, SMA is known to have further cognitive functions beyond simple motor timing and coordination (Apaydın et al. 2018; Altınok et al. 2023). Studies have shown activation of this area in many cognitive functions including but not limited to sequential task performance, ordering of stimuli, working memory, and speech (Cona and Semenza 2017). This could suggest the interaction we found only between time and number in this area is more on a higher cognitive function level.

Insula

Another significant activation likelihood cluster observed in conjunction analyses was in the anterior insula. A previous meta-analysis on space and number perception has found no activation of the insula for conjunction analyses (Hawes et al. 2019). Our results showed strong insula activation for all conjunctions. This area has been linked to task difficulty, error monitoring, salience network, as well as telling apart external stimuli from internal (Craig 2002; Hester et al. 2004; Craig 2009a; Uddin et al. 2014; Vatansever et al. 2020; Üstün et al. 2021). A model of human awareness proposes that the anterior insula functions to convert the interoceptive signals to behavioral results and also plays a role in self-environment discrimination (Craig 2009a). The activation observed in the anterior insula can be viewed in support of this model as both time and space perception are critical for the perception of the environment and this may be linked to self-awareness. Additionally, since task conditions are by nature harder than control conditions, activations in the insula can be attributed to task difficulty. However, for time perception, the insula has been suggested to track the gradual change in interoceptive signals to form a basis for perceiving time (Craig 2009b). We suggest that the anterior insula may have a more domain-specific role in space and number perceptions as well, and this area may be one of the cortical areas where the perceptions interact.

Triple conjunction analysis

The current work is the second meta-analysis study to analyze all three perceptions together, and the first to do so in a purely magnitude-oriented way. For this reason, we feel it is important to highlight the similarities and differences between our results and the only previous meta-analysis studying the conjunction of these three perceptions together (Cona et al. 2024). We did not conduct a gradient analysis; thus, it is impossible in this study to support or refute *Gradi*ATOM. Our results, however, can help uncover the function of the previously reported areas. Discussing the possible reasons for differences in the two meta-analyses along with the results of Skagerlund's fMRI study (2016) may help shine a light on the neural basis of magnitude perception.

In our conjunction results, we observed significant activation likelihood clusters in three cortical areas, which are the right inferior parietal lobule, right inferior frontal gyrus and right insula. Cona (2024) reported triple conjunction at SMA/ACC anterior cingulate cortex (ACC), bilateral insula, right inferior frontal gyrus and bilateral IPL. In their gradient analyses they found gradients in all regions except for the insula, for at least one pair of perceptions (Cona et al. 2024).

Our results reflect a more limited network compared to *Gradi*ATOM results. We believe this is because we chose to include only magnitude-oriented tasks and exclude higher-level cognitive tasks in our article selection. This might also explain why we found a right hemisphere activation while Cona (2024) found bilateral activations in some areas. Our results showed a more limited network compared to the results of a previous fMRI study on space, time, and number conjunction as well, but the predominantly right-lateralized activation patterns they found were quite similar (Skagerlund et al. 2016). This suggests that specifically the left hemisphere activations Cona (2024) found might reflect higher-level neural functions. Another difference is that we chose to exclude studies with less than 10 participants, while Cona (2024) included studies that had five or more participants. A low number of participants in fMRI studies can increase the possibility of false positives and the statistical errors of a study reflect directly onto a coordinate-based meta-analysis (Müller et al. 2018). We think that our results were more conservative in that aspect as well.

Our triple conjunction result did not show activations in the SMA. Cona (2024), however, found the right SMA activations and showed gradients for space–time and number–time conjunctions. Only our number and time perception analyses showed activations in SMA, which is also supported by the output of the conjunction analysis (Table 2, Fig. Fig. 1). It is interesting that our meta-analysis did not reveal any activation area in SMA for space while Cona et al. (2021) showed robust gradients in SMA for space and time. There could be two possible explanations for this discordance. The main difference our study had was that it included only perceptual studies; thus, the SMA activation for space perception might be related to higher-level functions, and the gradients previously found may also not necessarily reflect magnitude perception. On the other hand, when investigated further, we also noticed that with a lower statistical threshold, we could obtain SMA activations for space perception, implying that with a higher number of perceptual studies, our results could also resemble the results of Cona et al. (2024). This possibility is also supported by a previous fMRI study that found significant activation in the right SMA for space, time, and number conjunction (Skagerlund et al. 2016).

The cluster we observed in the right inferior parietal lobule is located in Brodmann's area 40, and its location is consistent with the IPS (Fig. 2). The right parietal lobe, implicated in distinct roles for each perception, holds a significant position in the literature on magnitude perception. When proposing the theory of magnitude perception, Vincent Walsh suggested the right parietal lobe as a key region for magnitude perception, based on various studies in animals and humans. He supported this suggestion by the observed activation of the inferior parietal cortex in studies related to all three perceptions and the disruption of all three perceptions in cases of damage to the right inferior parietal cortex (Walsh 2003; Bueti and Walsh 2009). In this context, the significant activation likelihood observed in the right inferior parietal cortex in our study was evaluated to be related to the magnitude aspect of all three perceptions. The shared activation in this region for perceptions supports the notion that the right inferior parietal cortex plays a crucial role in neural networks related to magnitude perception. Unlike Cona (2024), our results did not show a left IPL activation. Skagerlund et al. (2016) also didn't show any left hemisphere activation for IPL, which suggests left IPL activation may be related to higher-level cognitive functions.

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Our study identified a shared significant activation probability cluster for all three perceptions in the right inferior frontal gyrus, corresponding to Brodmann's area 9, and its location aligns with the IFJ (Fig. 2). This region is linked to top-down control of attention and is a part of the cognitive control network, which involves but is not limited to task switching and working memory update (Cole and Schneider 2007; Sundermann and Pfleiderer 2012). Studies on the functions of rIFJ are relatively few; thus, it is harder to hypothesize its function in certain cognitive processes. However, each of the studies we included had an active control task, in which participants were required to attend to a different aspect of a stimulus and make a response. In fMRI studies, control tasks used in addition to the primary tasks effectively act as another task for the participant. This task switching requires the working memory to update task rules and direct attention to different properties of the stimuli. In the context of task rule updating, this turns the control and task conditions together into one "task switching" condition. If the activation was caused only by working memory update and fMRI analysis logic, we would expect the activity to be the same in "task" and "control," and the subtraction would yield no activation in the area. Therefore, since our study involves contrasts between magnitude-based tasks and control tasks, our findings suggest that the observed activation cannot be explained solely by task switching but must have a component specific to the magnitude processing. What this component is and how it relates to visuospatial processing, magnitude judgments, action decisions, and higher cognitive processes is open to debate.

Insula, a crucial component of the saliency network, has been associated with error monitoring and task difficulty in previous studies (Hester et al. 2004; Uddin et al. 2014; Vatansever et al. 2020; Üstün et al. 2021). Additionally, it is linked to interoception, and it is suggested that the bilateral insular maps of interoception are remapped, particularly in the right anterior insular cortex, to facilitate the formation of self-awareness (Craig 2002). One perspective proposes that the anterior insular cortex is associated with the transformation of internal sensations into higher-order cognition, emphasizing its importance in distinguishing internal stimuli from external ones and directing attention to external stimuli (Craig 2009a). In the articles included in our analysis, all the tasks involved external stimuli, requiring participants to engage their attention externally to compare or reproduce magnitudes. While insula activation can be associated with directing attention to external stimuli, it is essential to note—again—that only contrasts with active control tasks were included in our analysis. In these control tasks, participants were presented with stimuli and required to provide a response, necessitating the external orientation of attention. The insula has a role in the salience network, but in our included studies, both conditions had a stimulus that would be described as salient for the task at hand. The inherently more challenging nature of the task conditions compared to the control condition is common for all three perceptions, and this could also be associated with the observed activation in the right anterior insula. However, in the studies we included, the only factor that can affect the difficulty of the task is the change in the feature of the stimulus the participant would need to attend to, such as the magnitude. In this context, the observed insula activation may represent a cognitive process related to magnitude perception, possibly the integration of externally presented stimuli's magnitude-related components with interoceptive stimuli.

Studies have shown that the insular cortex plays a role in recognition memory, contributing to the transformation of new information into familiar stimuli (Bermudez-Rattoni 2014). This function may also be part of its role in decision-making processes (Llorens et al. 2023). Specifically, in the context of magnitude perception, our findings suggest that the insular cortex might engage in a domain-specific recognition memory process, where it evaluates and integrates both existing knowledge about magnitude and new sensory information encountered during the task. This process could involve utilizing interoceptive signals to compare past experiences with present stimuli, thereby aiding in the assessment of magnitude. This would be in line with the notion that neural mapping and interaction of magnitude-related modalities are dependent on interactions with the environment (Walsh 2003; Bueti and Walsh 2009). Our results did not show a left insular activation, while Cona (2024) showed a conjunction in this area. Skagerlund et al. (2016) also showed a small cluster in the left insula for triple conjunction, which suggests that there's a need for more perceptual studies to verify the involvement of the left insula in magnitude perception, and clarify the possible function in the magnitude network.

A noteworthy finding in our study is that all identified clusters of significant activation likelihood for the three perceptions are located in the right hemisphere. Walsh, in his original formulation of the ATOM theory, divided magnitude perception into two cortical centers as posterior (parietal lobe) and anterior (prefrontal cortex), suggesting that the anterior system is more left-hemisphere dominant. He linked the left hemisphere dominance of the anterior system to linguistic functions (Walsh 2003;Hawes et al. 2019 ; Cona et al. 2021). Subsequent studies reported activations in both the right and left prefrontal cortices (Hawes et al. 2019; Cona et al. 2021). In an fMRI study evaluating all three perceptions together, activations were reported bilaterally in the prefrontal region, in areas corresponding to IFJ (Skagerlund et al. 2016). Additionally, a TMS study showed that the right inferior frontal gyrus plays a crucial role in the decision-making stage of magnitude perception (Hayashi et al. 2013a). In our study, prefrontal cortex activation was observed in the right IFJ region, deviating slightly from the original magnitude theory but aligning with recent literature.

The exclusive right hemisphere activation in our study implies that magnitude perception relies on neural networks with right hemisphere dominance. Studies on visual processing have shown an information flow from the primary visual cortex to the parietal cortex, then to the prefrontal cortex, concerning the perception of object locations in visuospatial perception. In this context, the parietal cortex was attributed a role in the high-level sensory association, while the prefrontal cortex was implicated in representing and processing spatial information (Takahashi et al. 2013). A similar neural network can be proposed for all magnitudes, starting from primary sensory areas and extending to the parietal cortex, terminating and being processed in the inferior frontal gyrus. In this hypothetical network, the parietal cortex would receive sensory information from primary visual areas and possibly other sensory information that can provide spatial cues of the environment, process and integrate each modality of continuous magnitudes in a partially overlapping neural network. At this stage, the processing could be done through multi-modal neurons found in the parietal cortex and have a symmetrical interaction. The processed information would then be sent to the right prefrontal cortex for a magnitude judgment. In this stage, memory and interoception could be a provider of critical information, integrated into basic sensation for a correct judgment or action decision. The influence of experience and language acquisition could, at this stage, make this interaction asymmetrical. No brain function is isolated from others, so the

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right prefrontal cortex connection with left hemisphere language networks would also need to be considered in the decision-making stage, and higher executive functions would be expected to have top-down control on the whole of magnitude processing. Parietal cortex neural activations would also be subject to control from prefrontal areas, and this bi-directional connectivity could explain the automaticity and working memory load effects on perceptual interactions. This hypothetical network would most probably be right hemisphere dominant, as it is the dominant hemisphere in spatial processing.

However speculative and vague it is, the proposed connectivity network is an idea worth exploring. This kind of network is accommodating of both ATOM and CMT on different cognitive levels, where they're not contradictory but complementary theories, which has been suggested before (Winter et al. 2015). Moreover, considering the developmental changes in magnitude representations, the link between ATOM and CMT could be found in the "Developmental Divergence Model" which suggests an innate common processing system for quantities that later divide into separable systems. In the context of the proposed network, though, this developmental change would refer to an underlying neural basis for common magnitude processing being present at birth, which, later in life, will be affected largely by experience, language, and learning (Dormal and Pesenti 2012; Newcombe 2014; Hamamouche and Cordes 2019).

Our study's results support the existence of a right-hemisphere-dominant network for magnitude perception. The nature of task-control contrasts in the studies included in our meta-analysis did not anticipate significant activation in primary sensory centers, making it difficult to make strong claims. However, the observed activations in the right hemisphere in the parietal, frontal, and insular cortices suggest the presence of a right-hemisphere-dominant neural network for magnitude perception. On the other hand, as a neuroimaging meta-analysis study, our study carries the limitations of the studies included in the analysis, such as false positives or smaller sample sizes. Additionally, the coordinate-based meta-analysis method we used shows the likelihood that a voxel will be activated with a given task. These results, while informative, do not show a direct connection between shown activation areas, nor do they indicate causality. They are also unable to provide any information on how these areas are connected functionally or anatomically. Further neuroimaging and connectivity studies are necessary to test the validity of our results and conclusions.

It is also important to note that our activation areas have been found in the conjunction analysis despite including magnitude-based control tasks. As previously mentioned, even though magnitude domains are thought to be partially integrated, the cognitive components aren't identical. Moreover, even if the neural basis for magnitude perception were mostly identical for all perceptions, there would be a nuance. The neural basis of brain functions was recently shown to be organized in hierarchically continuous gradients, and the recent advancement of *Gradi*ATOM was based on this notion (Margulies et al. 2016; Huntenburg et al. 2018; Cona et al. 2021). A gradient means that subtracting one from the other would result in not a complete disappearance of the BOLD signal, but a skew in the peak. If the functional activations for magnitude conjunctions work as gradients (Cona et al. 2021, 2024), the areas related to magnitude would still be seen as activated in a study with a magnitude-based control; even though the reported peak wouldn't be at the exact location, it could be with a non-magnitude control task. ALE analysis, as explained above, takes into consideration the locational deviations resulting from data collection and preprocessing steps, and creates a Gaussian activation probability sphere around the reported peak coordinate (Eickhoff et al. 2009, 2012; Turkeltaub et al. 2012). Thus, the information these studies provide would still be valuable, especially when calculated together with studies where control tasks are not magnitude related. Moreover, the areas that our conjunction analyses show to be relevant to both (or all three) perceptions were observed despite the limitation this methodological choice may bring, which makes our conjunction results more robust.

Conclusion

Our study focused on the possible brain areas for the common processing of the three magnitude perceptions to occur, as representation of magnitude can take place in such areas. Despite our strict exclusion criteria, our results indicate that space, time, and number perceptions may indeed occur through partially shared mechanisms, as the ATOM theory suggests, specifically the inferior fronto-parietal and insular brain regions. The observed activations were exclusively in the right hemisphere, which suggests the presence of a right-hemisphere-dominant neural network for magnitude perception.

Author contributions

Hazal Şimşek-Ünver (Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft), Burcu Sırmatel-Bakrıyanık (Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing—original draft), Beyza Doğanay (Methodology, Writing: review & editing), Fuat Balcı (Methodology, Formal analysis, Writing—review & editing), Metehan Çiçek (Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Writing: review & editing).

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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Conflict of interest statement. None declared.

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