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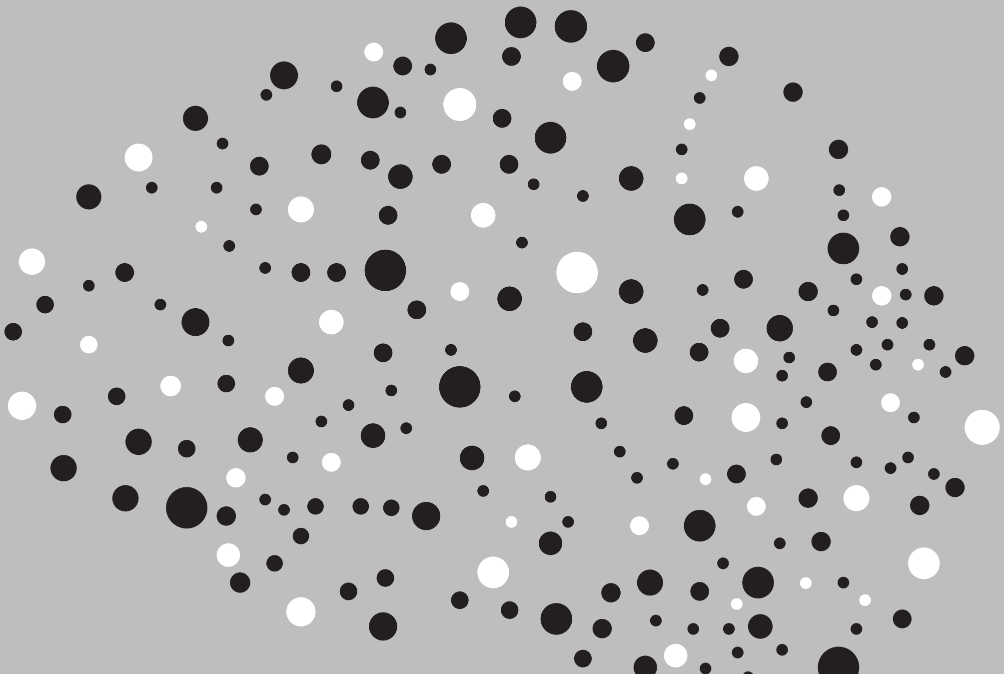
Neural selectivity and perception of numerosity and other quantities



Andromachi Tsouli

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Neural selectivity and perception of numerosity and other quantities

Blijf kijken voor meer (of minder)

Neurale selectiviteit en de waarneming van hoeveelheden en andere grootheden
(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad van doctor aan de
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op gezag van de
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ingevolge het besluit van het college voor promoties
in het openbaar te verdedigen op

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Andromachi Tsouli

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Prof. dr. S.F. te Pas

Table of Contents

Chapter 1 General Introduction 9

Chapter 2 Adaptation to visual numerosity changes neural numerosity selectivity 29

Chapter 3 Adaptation reveals unbalanced interaction between numerosity and time 51

Chapter 4 Distinct temporal mechanisms modulate numerosity perception 69

Chapter 5 The role of neural tuning in quantity perception 99

Chapter 6 General Discussion 119

Appendix

References 129
Supplementary materials 157
Summary in Dutch 189
Acknowledgments 199
List of publications 207
Curriculum Vitae 211

To my grandmother

Chapter 1

General Introduction

Numerosity as an evolutionary endowment

Imagine you are at the supermarket doing some last-minute grocery shopping. As you are approaching the checkout area, you notice that on the left aisle, there are customers waiting in line with shopping carts containing a few items, and on the right aisle, a customer with a shopping cart containing many items (Figure 1). You are late for work, and more people are approaching the checkout area, so you need to decide fast and efficiently which aisle to use. You choose the right aisle and hope that your estimation strategy works in your favor.

Figure 1. *Numerosity in everyday life.* When choosing which checkout aisle to use at the supermarket when we are in a hurry, we need to process and combine different numerical quantities or numerosities, such as how many checkout aisles are available, how many customers are ahead of us and how many items are within each customer's cart.

This is one of many examples in daily life where we use numerosity, the set size of a group of objects, in order to act optimally in our environment. Numerosity refers to the cardinality of objects and is to be distinguished from symbolic numerosity or nominal number (e.g., 'number thirteen') which is an exclusively language-dependent human ability. Our capacity to process numerosity non-verbally is considered to have evolved in order to facilitate our ability to navigate, exploit food sources, and avoid predation (Nieder, 2020b). Evidence for this evolutionary system of numerosity processing comes from cross-cultural investigations as well as developmental and animal studies. More specifically, indigenous Amazon communities such as the Pirahã who use a "one-two-many" system of counting or the Mundurukú who lack words for numbers beyond five, can still approximate numerical quantities beyond their counting system (Gordon, 2004; Pica et al., 2004). Developmental studies show that humans are born with a rudimentary ability to process numerical quantities which becomes more refined with increasing age. Specifically, infants can perceive abstract numerical quantities from the moment of birth (Izard et al., 2009). At six months of age, infants can discriminate between numerosities differing by a 1:2 ratio (e.g., 4 vs. 8 or 8 vs. 16 dots) (Feigenson et al., 2004; Xu, 2003; Xu & Spelke, 2000) but not a 2:3 ratio which is achieved at 10 months of age (Xu & Arriaga, 2007). In adulthood, humans can accurately discriminate numerosities differing by a 9:10 ratio (Halberda & Feigenson, 2008). Evidence from comparative psychology suggests that a number of species such as macaques (Brannon & Terrace, 2000; Nieder & Merten, 2007; Nieder & Miller, 2003), corvids (Ditz & Nieder, 2016), fish (Agrillo & Bisazza, 2017), amphibians (Krusche et al., 2010), and insects (Giurfa, 2019) can discriminate specific numerosities. Hence, numerosity perception does not necessitate the use of linguistic labels as previously theorized (Carey, 2000; Chomsky, 1988), but appears to have evolved from a biological precursor system which equips humans and animals with an intuitive understanding of numerical quantities. **But how exactly do we process numerosity**? A number of different accounts have been proposed and below are some of the most influential theories in the field of numerosity perception.

Numerosity as a derivative of non-numerical cues

If we go back to the example where we are trying to decide which checkout aisle to use at the supermarket, some theorists would argue that it is not numerosity per se that determines our judgment of quantity but non-numerical perceptual properties which covary with numerosity (Allik & Tuulmets, 1991; Gebuis et al., 2016; Leibovich et al., 2017). For example, a checkout aisle occupied by 5 people will be judged as more numerous compared to an aisle occupied by 2 people since the former will cover more of the visual scene due to the total surface of the number of people and the area they occupy. Gebuis and colleagues (2016) proposed that numerosity judgements are based solely on non-numerical sensory cues present in numerosity stimuli such as density, surface area, and convex hull, and that the integration of these cues is what forms the basis of numerosity comparisons. A similar theory by Leibovich and colleagues (2017) posits that it is impossible to examine numerosity processing in isolation from continuous features (e.g., size, area, and density) and that perception of these non-numerical features is more innate and automatic than perception of numerosity itself. Despite the plausibility of these theories, the interplay between non-numerical cues and numerosity does not refute the existence of a dedicated system for numerosity perception as supported by electrophysiological, neuroimaging and psychophysical evidence which I will discuss shortly (see also extensive peer commentary on Leibovich et al., 2017).

Distinct processing mechanisms for distinct numerosity ranges

It has been suggested that there are three distinct (but overlapping) processing mechanisms subserving numerosity perception depending on the numerosity ranges to be estimated (Anobile et al., 2016; Feigenson et al., 2004).

The first mechanism known as ‘subitizing’ (Kaufman et al., 1949) or ‘object tracking system’ (Feigenson et al., 2004; Piazza, 2010) is considered to underlie the fast and error-free perception of very low numerosities (up to 3 to 4 items; ‘subitizing range’) without the need for counting. A number of behavioral studies seem to support the notion that subitizing is a distinct numerosity processing system based on discontinuities in accuracy and reaction time when processing very low compared to higher numerosities (Atkinson et al., 1976; Choo & Franconeri, 2014; Kaufman et al., 1949; Mandler & Shebo, 1982; Pomè et al., 2019; Revkin et al., 2008). Similar findings showing errorless performance in the enumeration of very low numerosities have also been found in the auditory (Camos & Tillmann, 2008; Repp, 2007) and haptic modality (Plaisier et al., 2009; Riggs et al., 2006). Nevertheless, whether discontinuities in the assessment of low versus high numerosities reflect the existence of distinct numerosity systems is not universally accepted (Cheyette & Piantadosi, 2020; van Oeffelen & Vos, 1982). Instead, a number of studies provide support for the existence of a single mechanism underling the representation of both low and high numerosities (Balakrishnanl & Ashby, 1992; Cai et al., 2021; Cordes et al., 2001; Nieder & Merten, 2007; Sengupta et al., 2017).

The second mechanism is called the ‘approximate number system’ (ANS) or analogue magnitude representation and is considered to underlie the ability of humans and animals to represent the approximate number of objects in their environment as imprecise, noisy mental magnitudes (Dehaene, 2011; Feigenson et al., 2004; Gallistel & Gelman, 2000). The most defining characteristic of the ANS is that the imprecision of its numerical representations increases with increasing numerical magnitude in such a way that two numerical quantities can be discriminated only if they differ by a given numerical ratio (Piazza, 2010). In other words, numerosity discrimination performance is modulated by the ratio of the numerical quantities rather than their absolute difference. This ratio-dependent performance has been shown in adults (Halberda & Feigenson, 2008; Pica et al., 2004; Whalen et al., 1999), infants (Lipton & Spelke, 2003; Xu & Spelke, 2000) and animals (Cantlon & Brannon, 2007; Jordan & Brannon, 2006). The ANS is also considered to underlie exact, symbolic numerical representations (e.g., 8, “eight”) and the development of mathematical abilities (Dehaene, 1992, 2001a; Feigenson et al., 2004; Piazza, 2010). One line of evidence comes from studies showing that children with developmental dyscalculia, a neurodevelopmental learning disability that causes severe difficulties in the acquisition of arithmetic skills and number processing, have lower ANS acuity (Mazzocco et al., 2011; Piazza et al., 2010). Nevertheless, whether the ANS is an integral component of mathematical abilities and developmental dyscalculia is currently under debate (see review by Szkudlarek & Brannon, 2017).

The third mechanism is called the "texture/density" and is considered to operate when the number of items is so high that they blur into a texture or when numerosity stimuli are presented at an eccentricity where they become "crowded" (Anobile et al., 2016). As proposed by Anobile and colleagues (2016), texture mechanisms come into play when object segmentation is prevented (e.g., by means of crowding), and it is only then that numerosity stimuli will be perceived as a texture rather than individual items. This notion is further related to psychophysical evidence showing how numerosity judgements are influenced by density, indicating that numerosity and density might rely on common visual mechanisms (Dakin et al., 2011; Durgin, 1995).

Neuroanatomical correlates of numerosity processing

When examining the neural underpinnings of numerical processing, early neuropsychological and neuroimaging studies focused on uncovering the neural underpinnings of symbolic numerosity processing (e.g., Arabic numerals). Patients with lesions in fronto-parietal (Cipolotti et al., 1991) and intra-parietal cortical areas (Dehaene & Cohen, 1997; Takayama et al., 1994; Warrington, 1982) exhibit impaired mental manipulation of numbers. Single-cell recordings in Parkinson's patients have further revealed neurons in the parietal cortex which responded selectively during counting and arithmetic operations (Abdullaev & Melnichuk, 1996). The role of the parietal cortex in number processing was also confirmed by functional imaging studies in healthy participants who show increased activation in parietal and prefrontal areas (Dehaene et al., 1996; Roland & Friberg, 1985), and specifically in the intraparietal sulcus (IPS), during mental arithmetic (Chochon et al., 1999; Pinel et al., 2001; Simon et al., 2004) or number detection (Eger et al., 2003).

Based on these findings, it was speculated that the parietal cortex holds a "biologically determined representation" of numerical quantity (Dehaene et al., 1998, p. 360). As such, parietal areas should also be activated during non-symbolic numerosity processing. This was confirmed by subsequent functional magnetic resonance imaging (fMRI) studies. FMRI is an indirect measurement of the activation of neural populations. With increased neural activity, there is increased oxygen extraction from the blood. By measuring changes in the oxygen concentration, the so-called blood-oxygen-level-dependent (BOLD) response, fMRI can infer neural responses elicited by a given stimulus (Logothetis, 2003; Logothetis

& Wandell, 2004). Using this method, it was shown that numerosity estimation of visual or auditory sequences was associated with increased activity in a right lateralized fronto-parietal cortical network. Similarly, BOLD activity in the IPS and postcentral sulcus was shown to increase with increasing difficulty in a numerosity estimation task (Castelli et al., 2006). Parietal areas, including the superior part of IPS, were shown to be involved in numerosity perception even in the absence of an explicit task or response requirements (Ansari et al., 2006). The role of parietal areas and the IPS in non-symbolic numerosity processing was further illustrated in 4-year old children, with the authors suggesting that the IPS might serve as the basis upon which symbolic number processing is constructed (Cantlon et al., 2006).

A "sense of number" and neural tuning to numerosity

Given how humans and animals are endowed with an intuitive understanding of numerical quantity or "number sense" (Dantzig, 1930; Dehaene, 2011), it is suggested that numerosity perception is supported by the activity of neural populations which respond preferentially or are 'tuned' to specific numerosity ranges (Burr & Ross, 2008; Dantzig, 1930; Dehaene, 2011; Nasr et al., 2019; Viswanathan & Nieder, 2013). Converging evidence from animal electrophysiology, fMRI, and psychophysics provides support for the existence of neural populations which respond selectively to specific numerosity ranges.

Single-cell recordings reveal numerosity-tuned neurons.

In the 1960's, single-cell recordings in cats revealed for the first time the existence of neurons which fired after a certain number of events, irrespective of whether these events were presented in the visual (e.g., 3 flashes of light) or auditory (e.g., 3 tones) modality (Thompson et al., 1970). Three decades later, single-cell recordings in macaques revealed neurons in the prefrontal (Nieder et al., 2002; Nieder & Miller, 2003) and parietal cortex (Nieder & Miller, 2004a) which were selective to visual numerosity. Each recorded neuron showed maximum activity or tuning for one of the numerosities presented and a progressive drop-off in activity as the numerosity varied from the 'preferred' numerosity (Nieder et al., 2002; Figure 2a & 2b). The authors also tested a number of control conditions by varying the physical appearance (e.g., surface area or density) of the numerosity stimuli and illustrated that the majority of recorded neurons were tuned to numerosity, irrespective of the physical appearance of the stimuli (Nieder et al., 2002). The existence of these neurons was later confirmed in corvids (Wagener et al., 2018) as well as humans (Kutter et al., 2018). Further research revealed neurons tuned to both visual and auditory numerosity (Nieder, 2012), supporting the notion of an abstract, 'supramodal' neural code for numerosity. In addition, numerosity-tuned neurons were present in both trained and numerically naïve macaques, speaking in favor of a "number sense" (Viswanathan & Nieder, 2013). While the above-mentioned studies showed neural tuning to very low numerosities (1 to 5 items), subsequent research revealed neurons with preferred numerosities covering the entire range between 1 and 30 items, arguing in favor of a single encoding mechanism for low and high numerosities (Nieder & Merten, 2007).

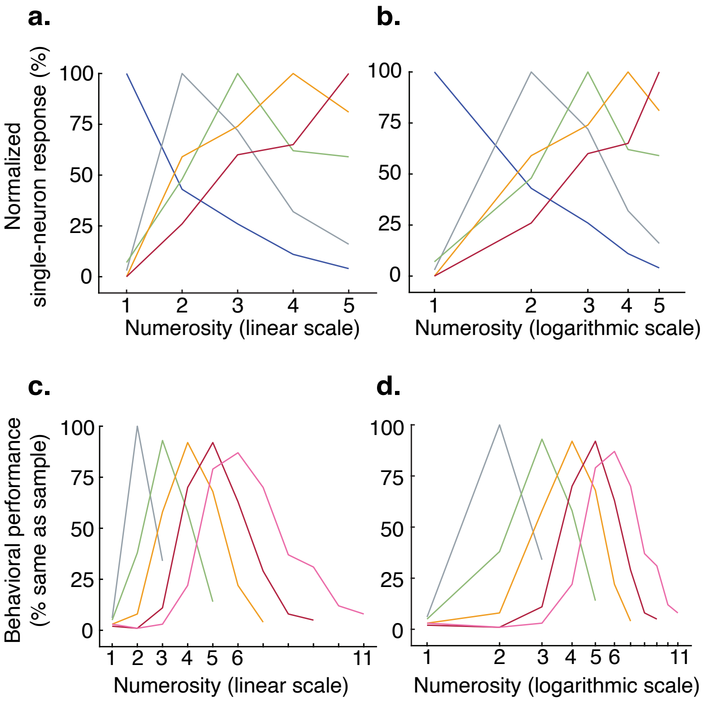

Figure 2. *Neural and behavioral numerosity tuning curves.* (a) Normalized responses of numerosity-tuned neurons recorded from the prefrontal cortex of macaques during the sample period (first display of each numerosity stimulus) of a visual numerosity judgment task. Numerosity tuning curves are asymmetric, with increasing width on a linear scale. (b) When plotted on a logarithmic scale, numerosity tuning curves become more symmetric with constant width across different numerosities. (c, d) The same tuning profile was observed in behavioral performance, where macaques indicated whether the test numerosity stimulus had the same number of items as the first numerosity stimulus shown. These findings show a correspondence between neural and behavioral numerosity representations which appear to follow a non-linear, compressed coding scheme similar to that of other sensory phenomena (Drawn after: Nieder & Miller, 2003).

When examining the underlying properties of neural numerosity tuning, it was also shown that when plotted on a linear scale, both neural and behavioral numerosity tuning curves are asymmetrical, with different width for each numerosity (Nieder & Miller, 2003; Figure 2a & 2c). When plotted on a logarithmic scale, numerosity tuning curves become symmetrical with constant tuning width or variability across numerosities (Nieder & Miller, 2003; Figure 2b & 2d). Hence, the authors suggested that numerosity processing is based on an analog magnitude representation of numerical quantity whose coding scheme follows that of other sensory phenomena such as weight or luminance (Fechner, 1860; Weber, 1834). These findings were also in accordance with proposed models of numerosity encoding, according to which successive numerosities are represented on a logarithmically compressed scale with fixed variability across different numerosities (Dehaene, 2001b; Dehaene & Changeux, 1993; van Oeffelen & Vos, 1982).

FMRI adaptation hints at the existence of neural numerosity tuning in humans.

In humans, neural numerosity tuning was first shown indirectly using fMRI adaptation (Piazza et al., 2004). FMRI adaptation, also referred to as repetition-suppression, follows the assumption that the activity of neurons tuned to a specific numerosity is decreased or suppressed after repeated presentation of the same, 'adapted' numerosity, whereas the activity of neurons tuned to different numerosities is less affected (Grill-Spector et al., 2006; Larsson et al., 2016). Hence, after the presentation of the adapted numerosity there is decrease in the recorded fMRI signal, while after the presentation of numerosities different ('deviant') from the adapted numerosity there is release from adaptation and fMRI signal recovery. By calculating the difference in the fMRI signal recorded during the presentation of the adapted and deviant numerosities, Piazza and colleagues (2004) showed (inverted) numerosity tuning curves with logarithmic scaling in the parietal cortex, providing support for the existence of neural numerosity tuning previously reported in macaques (Nieder & Miller, 2004a; Viswanathan & Nieder, 2013).

Ultra-high field fMRI reveals topographic representation of numerosity.

Neural numerosity tuning and its cortical organization were since measured more directly by Harvey and colleagues (2013) using ultra-high field (7 Tesla) fMRI and biologically-inspired neural model-based analyses (population receptive field [pRF] modeling) (Dumoulin & Wandell, 2008; Wandell & Winawer, 2015). The authors used a numerosity stimulus sequence of 1 to 7 dots, with a baseline condition of 20 dots, and measured a number of control conditions where for example, the total dot area, individual dot size or total dot circumference were kept constant. Participants did not have to perform any numerosity judgements, but simply report when the color of the dot stimuli switched from black to white. The recorded fMRI responses were analyzed using numerosity-selective pRF models which summarize the responses of numerosity-tuned neural populations within a cortical location. The study showed for the first time, neural populations tuned to low numerosities in the (right) posterior parietal cortex which are organized in a highly ordered manner, forming a topographic numerosity 'map' (Figure 3).

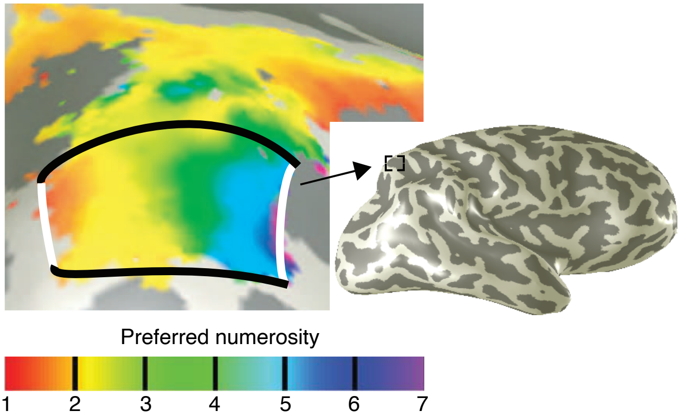

Figure 3. *Topographic numerosity map in the posterior parietal cortex.* Highlighted region in the right posterior parietal cortex where neural populations showed numerosity tuning. Numerosity-tuned responses form an orderly topographic map, i.e., a region where preferred numerosity changes gradually across the cortical surface, with preferred numerosity increasing from medial to lateral regions of the map (Drawn after: Harvey et al., 2013).

While topographic maps had been previously established in sensory systems such as vision (visual field maps; Wandell et al., 2007) and audition (tonotopic maps; Kaas & Hackett, 2000), the study of Harvey and colleagues (2013) was the first to show a topographic map for an abstract feature such as numerosity. Moreover, this numerosity map was robust to changes in the features of the visual numerosity stimuli, as confirmed by further computational analyses (Harvey & Dumoulin, 2017b, 2018). Subsequent studies revealed the existence of six widely separated topographic numerosity maps in the left and right hemisphere (Harvey & Dumoulin, 2017a), as well as a continuous neural representation of low and high numerosity preferences covering subitizing and estimation ranges within the same numerosity maps (Cai et al., 2021). More recently, topographic numerosity maps were also found for haptic numerosity (number of hand-held objects) in cortical and subcortical areas (Hofstetter et al., 2021; Hofstetter & Dumoulin, 2021).

Numerosity tuning shown using psychophysics and adaptation.

The existence of a distinct neural system dedicated to numerosity perception has been inferred using psychophysics and adaptation. In psychophysics, adaptation examines how recent sensory history affects perceptual experience through the repeated presentation of a particular stimulus which makes subsequently presented stimuli appear more different from the adapter than they are (Frisby, 1979; Kohn, 2007; Mollon, 1974; Thompson & Burr, 2009). This method has been used extensively to study the visual coding mechanisms of primary visual properties such as spatial frequency (Blakemore et al., 1970), orientation (Clifford et al., 2000; Gibson & Radner, 1937), and motion (Wohlgemuth, 1911). All these visual properties are susceptible to adaptation, and in each case, the tuned neural responses inferred using adaptation and psychophysics were later corroborated by electrophysiology (spatial frequency tuning: Tolhurst et al., 1981; orientation tuning: Albright, 1984; motion tuning: Zeki, 1974).

Adaptation is considered a powerful tool to probe the neural substrates underlying perception of a given sensory dimension and further reveal its neural organization (Mollon, 1974). Specifically, adaptation relies on the principle that a given stimulus parameter is encoded by populations of neurons or 'channels' which are tuned to different values of that parameter, and have distinct but overlapping tuning curves. Repeated or prolonged exposure to a specific stimulus value is considered to suppress the response of neurons tuned to that value, with the extent of suppression depending on how strongly said neurons respond to that value (Clifford et al., 2000; Jin et al., 2005; Thompson & Burr, 2009). The hallmark of this adaptation-induced change in neural responses is that it is selective, since neural responses are suppressed for values similar to the adapted value but not for sufficiently different ones (Webster, 2015). This selective response suppression is considered to shift the value of the encoded stimulus parameter away from of the adapted stimulus which then predicts "repulsive" perceptual aftereffects when testing values which are slightly below or above the adapted level (Webster, 2011). Hence, adaptation is a valuable method for examining experience-dependent perceptual plasticity which can be linked to adaptation-induced plasticity of neural tuning to a given sensory property (Dragoi et al., 2000, 2001; Kohn & Movshon, 2004; Tolias et al., 2005).

Burr and Ross (2008) were the first to show the existence of the **numerosity aftereffect** in the visual modality. Specifically, adaptation to a high numerosity stimulus leads to underestimation of the numerosity stimulus subsequently presented in the adapted location (Figure 4a-b), whereas adaptation to a low numerosity leads to overestimation. This effect was shown to be spatially specific and occurring even when using very brief periods of adaptation (e.g., 250 ms) and few trials (Aagten-Murphy & Burr, 2016). On a neural level, this repulsive aftereffect pinpoints to the existence of neural populations tuned to different numerosities (Figure 4c). For example, adaptation to numerosity 80 leads to maximum response suppression of neural populations tuned to that numerosity and moderate response suppression of populations tuned to numerosity 40, whereas the response of populations further away from the adapted stimulus is not affected (Figure 4d). This changes the peak response or preferred numerosity of populations tuned to numerosity 40, which now shifts away from the adapted numerosity and towards a lower numerosity (e.g., 30; Figure 4e). This change is considered to underly the repulsive numerosity aftereffect, where numerosity 40 is perceived to be less numerous than it actually is after adaptation.

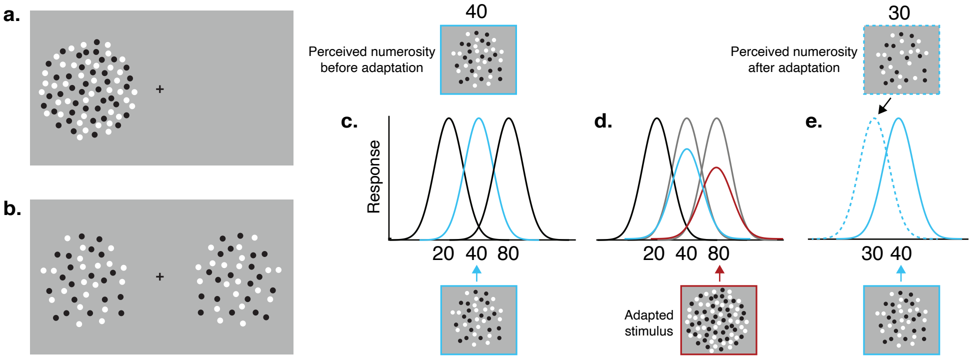

Figure 4. *Numerosity adaptation aftereffect and hypothesized neural mechanisms.* (a-b) After prolonged exposure to a high numerosity (80), a lower numerosity (40) presented in the adapted location (left) appears less numerous than it actually is when compared to the numerosity (40) presented in the unadapted location (right). (c) At a neural level, and before adaptation, the response of neural populations or 'channels' tuned to numerosity 40 (blue) is unaltered, and perception matches the presented stimulus. (d) During adaptation to numerosity 80 (red), there is great reduction in the response of neural populations tuned to that numerosity, a small reduction in the response of neural populations tuned to numerosity 40, and no change in the response of neural populations tuned to lower numerosities (20; black). Neural populations tuned to lower numerosities will now produce a greater response than neural populations tuned to 40 or 80. (e) This leads to a shift of the population response away from the numerosity of the adapted stimulus, and the neural responses previously encoding 40 are now encoding a lower numerosity (e.g., 30). This shift of the population response away from the adapted numerosity is considered to underly the shift of the phenomenal appearance of 40 away from the adapted stimulus, where 40 is perceived to be less numerous (e.g., 30) after adaptation.

Based on their discovery of the numerosity aftereffect, Burr and Ross (2008) argued that numerosity is a primary visual property and that humans are equipped with a visual sense of number. These findings were soon criticized as being an "elegant replication" of findings showing that adaptation to texture density influences numerosity perception, and that the reported numerosity aftereffect is in fact a density aftereffect (Durgin, 1995, 2008; see also Dakin et al., 2011; Tibber et al., 2012). Subsequent psychophysical research addressed this remark and provided strong evidence for the existence of a dedicated system for numerosity perception by illustrating that texture mechanisms come into play only when individual items are densely packed so that they cannot be perceptually segregated (Anobile et al., 2014, 2015, 2016; Arrighi et al., 2014; Burr et al., 2017; Cicchini et al., 2016; Ross & Burr, 2010). Moreover, and in agreement with the existence of an abstract representation of numerosity, further psychophysical studies showed numerosity adaptation aftereffects across spatiotemporal presentation formats (Arrighi et al., 2014) and in different sensory modalities (auditory: Arrighi et al., 2014; tactile: Togoli & Arrighi, 2021). Nevertheless, the neural implications of the numerosity adaptation aftereffect are not well understood. Specifically, it is currently unclear whether the perceptual effects of numerosity adaptation are linked to changes in the tuning profile of the numerosity-selective neural populations.

Numerosity as part of a generalized quantity system

Imagine you are trying to cross a busy road in the Dutch city of Utrecht. On your left, five cyclists are approaching at fast speed, and on your right, two cars and one bus have stopped at the traffic light which is about to change color any second now. You decide to cross the road the moment the bike lane is clear and before the traffic light for vehicles turns green. It becomes evident that in order to act optimally, you need to combine information about different quantities such as numerosity, time and spatial extent (e.g., physical size, length and distance). Processing continuous quantities such as time and space is a fundamental aspect of how humans and animals structure their environment and is essential for survival by e.g., facilitating anticipation and prediction of events, and navigation (Dehaene & Brannon, 2011). The ubiquitous nature of continuous quantity processing is supported by research findings showing that different animal species (Gallistel, 1989) and humans from early developmental stages (Brannon et al., 2006; de Hevia et al., 2014; Lourenco & Longo, 2011; VanMarle & Wynn, 2006) are equipped with representational mechanisms for temporal and spatial quantities, similarly to numerical quantity.

The case of time.

Time remains one of the most elusive and multifaceted quantities, and uncovering its neural and computational underpinnings is characterized as the "Holy Grail" of time research (Matell, 2014). There are different timescales of temporal processing ranging from microseconds to circadian rhythms (Mauk & Buonomano, 2004). In this thesis, I focus on time intervals primarily in the sub-second range, also called perceptual timing (Buonomano & Karmarkar, 2002).

Processing of time intervals in the range of hundreds of milliseconds is an essential part of our sensory experience, and used for speech recognition, motor control and music perception, to name a few (Mauk & Buonomano, 2004). Early theoretical models in psychophysical literature proposed that temporal judgements rely on the existence of a single internal clock (Creelman, 1962; Treisman, 1963; Treisman et al., 1990), which is centralized and 'amodal', and thus, used to extract the duration of a stimulus irrespective of sensory modality. These models are challenged by more recent findings and the so-called "distributed" timing models which, although diverse, share the principle that temporal processing is distributed among different brain areas which are deployed depending on the length of temporal intervals, the sensory modality in which they are presented, and the nature of the temporal task (Bruno & Cicchini, 2016; Bueti, 2011; Burr et al., 2007; Johnston et al., 2006; Mauk & Buonomano, 2004; Morrone et al., 2005).

Consistent with the idea of distributed timing mechanisms are theoretical accounts postulating the existence of time-selective neural substrates, where temporal information is encoded by separate channels or neural populations tuned to specific, preferred durations (Buonomano & Laje, 2010; Ivry, 1996; Matell & Meck, 2004; Wright et al., 1997). And while this channel-based or neural tuning approach of time interval processing is still in its infancy, evidence from electrophysiological, psychophysical, and fMRI studies provides support for the existence of duration-tuned mechanisms.

Electrophysiological studies in animals have revealed neurons tuned to time intervals of a few hundred milliseconds in the prefrontal cortex, striatum (Jin et al., 2009) and supplementary motor area of macaques (Merchant et al., 2013; see also Mita et al., 2009 for duration tuning in the range of seconds), and in the visual cortex of cats (Duysens et al., 1996). In humans, duration tuning was first inferred using psychophysics and adaptation (Heron, Aaen-Stockdale, et al., 2012). Adaptation aftereffects had been previously reported for other temporal dimensions such as auditory rhythm (i.e., train of beats; Becker & Rasmussen, 2007) and temporal frequency (Johnston et al., 2006) but not for single duration intervals. Heron and colleagues (2012) showed the existence of the duration aftereffect, where the repeated presentation of a short (160 ms) versus long (640 ms) duration leads to over- versus underestimation of a subsequently presented duration respectively, in a modality-specific way (Heron, Aaen-Stockdale, et al., 2012). Subsequent studies on duration adaptation further corroborated the existence of the duration aftereffect which does not appear to be spatially specific (Maarseveen et al., 2017), and corresponds to the onset and offset duration of the adapter and not the perceived duration of the adapted stimulus (Maarseveen et al., 2019). Moreover, the duration aftereffect has been shown to occur in sub-second and supra-second duration ranges (Shima et al., 2016), and is also present in the tactile modality (Li et al., 2019).

Duration tuning in humans was also illustrated using fMRI and an adaptation paradigm (Hayashi et al., 2015). Repeated presentation of a (short) duration stimulus was associated with maximum response suppression of neural activity in the right intraparietal lobule and gradual response recovery with increasing difference between the adapted and test durations (see also Hayashi & Ivry, 2020). Two subsequent ultra-high field (7 Tesla) fMRI studies showed for the first time the existence of duration-tuned neural populations which are organized topographically (Harvey et al., 2020; Protopapa et al., 2019). Protopapa and colleagues (2019) reported 'chronotopic' maps primarily located in the supplementary motor area, which appear to encode durations in a relative manner, changing in size and tuning profile depending on the duration range tested. Harvey et al. (2020) showed neural responses tuned to specific ranges of visual event timing in a number of cortical areas, where timing preferences change gradually, forming a network of topographic timing maps. The authors also reported that although these timing maps largely overlap with the network of numerosity maps previously identified (Harvey et al., 2015; Harvey & Dumoulin, 2017a), timing and numerosity maps appear to be distinct.

Based on the above, it becomes evident that time and specifically interval timing, shows commonalities with numerosity, based on electrophysiological, psychophysical and neuroimaging studies showing how the encoding of each quantity could be mediated by tuned neural mechanisms.

It has been suggested that numerosity and time rely on a common representational mechanism (Bonn & Cantlon, 2012; Cantlon et al., 2009; Meck & Church, 1983; Walsh, 2003). Meck and Church (1983) proposed a common 'internal accumulation mechanism' for evaluating numerical and temporal quantities after finding that rats are similarly sensitive to both numerosity and duration. In subsequent experiments, the authors reported a measurable quantitative equivalence between the number of stimulus segments and the duration of a stimulus (Meck et al., 1985). Inspired by Gallistel and Gelman (2000) who argued that numerosity and time draw upon a generalized magnitude system that represents these dimensions with a common underlying code, Walsh (2003; Bueti & Walsh, 2009) proposed the '**a theory of magnitude**' **(ATOM)**. This theory postulates that numerosity and time (among other quantities) may be computed according to a common metric because of the critical need of encoding these variables for action (Figure 5a). Furthermore, ATOM predicts a monotonic mapping of numerosity and time (see also Cantlon et al., 2009), with shared neural substrates in the inferior parietal cortex binding the computations for these quantities.

Hence, and according to the most literal interpretation of this theory, there should exist neurons which encode more than one type of quantity, and in this case, neurons tuned to both numerosity and time (Figure 5b). The primary evidence in support of the above-mentioned theories comes from neuroimaging studies showing overlapping brain activations when processing numerical and non-numerical quantities, particularly in the IPS (see meta-analyses by Cantlon et al., 2009; Cohen Kadosh et al., 2008; Sokolowski et al., 2017).

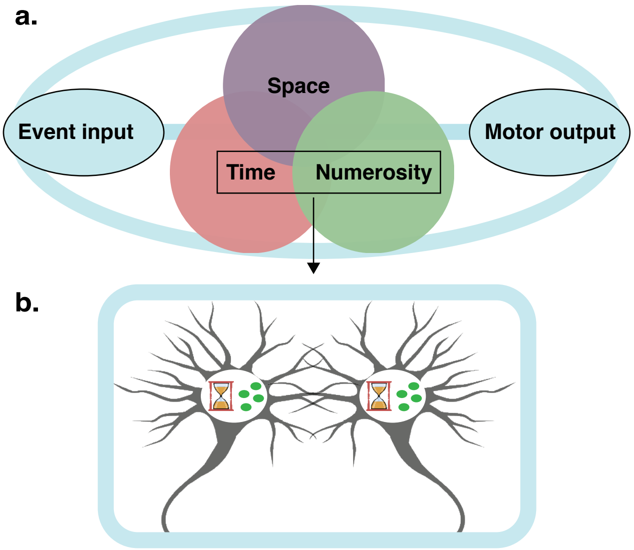

Figure 5. *A common magnitude system based on the ATOM theory and neural implications.* (a) According to ATOM, quantities such as numerosity and time are processed using a common cortical metric located in the parietal cortex, because of the need to encode these variables for action (Drawn after: Walsh, 2003). (b) At a neural, a common cortical metric implies the existence of neurons which encode both numerosity and time, and could therefore, be tuned to both types of quantities.

Behavioral evidence on the interaction of numerosity and time as part of a common magnitude system suggest a complex, if any, relationship between these quantities, with either a unidirectional effect of (non-symbolic) numerosity on duration judgements (Alards-Tomalin et al., 2016; Cappelletti et al., 2009; Chun et al., 2018; Dormal et al., 2006; Dormal & Pesenti, 2013; Droit-Volet et al., 2008; Hayashi, Valli, et al., 2013; Schlichting et al., 2020; Xuan et al., 2007), a unidirectional effect of duration on numerosity judgements (Lambrechts et al., 2013; Martin et al., 2017), a bidirectional effect (Javadi & Aichelburg, 2012), or no effect at all (Agrillo et al., 2010).

Despite the value of relevant neuroimaging and behavioral studies, the question of whether numerosity and time processing rely on shared neural substrates remains, since no study so far has confirmed or refuted the existence of neural mechanisms tuned to both numerosity and time which could underly perception of both quantities.

Thesis outline

The general research goal of this thesis is to examine the properties of numerosity-tuned neural populations (**Chapter 2**), and numerosity perception as part of a generalized quantity system by investigating the possibility of shared, tuned mechanisms between numerosity and time (**Chapters 3** and **4**), and other quantities and sensory modalities (**Chapter 5**).

In **Chapter 2**, we build upon previous research findings (Harvey et al., 2013; Harvey & Dumoulin, 2017a) showing the existence of topographically organized neural populations tuned to visual numerosity in the human brain. Specifically, we examine whether neural tuning to visual numerosity within the network of numerosity maps can be altered by numerosity adaptation. We hypothesized that if neural populations' tuning is affected by adaptation, then their preferred numerosity would change depending on both the presence and the numerosity of the adapter. We scanned participants using ultra-high field (7 Tesla) fMRI and analyzed the responses using custom-build pRF neural models of numerosity encoding. We replicated previous studies by showing the existence of several topographic numerosity maps. We further show that neural numerosity tuning is altered systematically in all numerosity maps during numerosity adaptation. We propose that these changes in neural numerosity tuning could potentially underlie the perceptual effects of numerosity adaptation.

In **Chapter 3**, we investigate whether numerosity and time rely on common neural mechanisms using psychophysics and a cross-adaptation paradigm. We reasoned that if numerosity and time perception rely on neural substrates which are tuned to *both* types of quantities, then adaptation to visual numerosity should affect visual duration perception, and adaptation to visual duration should affect visual numerosity perception. We replicated previous findings by showing that numerosity and duration are susceptible to adaptation. We further show that adaptation to duration produces a repulsive perceptual aftereffect in numerosity perception, whereas adaptation to numerosity does not significant affect duration judgments. We suggest that numerosity and time processing rely on *partially* overlapping neural networks.

In **Chapter 4**, we explore further the effect of adaptation to duration on numerosity perception we describe in Chapter 3, by conducting two follow-up experiments using psychophysics and adaptation. In the first experiment, we test the effect of adaptation to visual duration on visual numerosity perception, and in the second experiment we test the combined effect of adaptation to visual duration *and* numerosity on visual numerosity perception. We manipulated the onset/offset duration of the adapter, the adapter's total presentation time and the total duration of the adaptation trial. We hypothesized that if the effect of duration on numerosity reflects the adaptation of duration channels tuned to specific durations, then the adaptation effect will be driven by the onset-offset duration of the adapter. Conversely, if the effect of duration reflects the strength of adaptation of numerosity channels only, then the adaptation effect will be driven by the total duration of the adaptation trial, regardless of the onset-offset duration of the adapter. We show that the effect of adaptation to duration on numerosity perception is driven by adapting specific duration channels. In contrast, the effect of adaptation to numerosity on numerosity perception is driven by the total duration of the adaptation trial. We propose that distinct temporal mechanisms are involved in adaptation to duration compared to adaptation to numerosity.

In **Chapter 5**, we extend the role of neural tuning in numerosity perception to other quantities and sensory modalities. We advocate that neural tuning is the neural basis of quantity processing and is critical to understanding quantity perception. Our hypothesis is built on established theories in vision science and ties together recent results of animal electrophysiology, human neuroimaging and psychophysics with quantity perception. We argue that the tuning profiles of quantity-tuned neurons are closely linked to perception and underly seminal psychophysical laws and behavioral phenomena in quantity perception. We further propose that neural tuning is the basis for perceptual interactions between different quantities and modalities. Based on this, we suggest that observed commonalities in neural and behavioral representations between quantities are not accounted for by the existence of neural populations tuned to multiple quantities, but by the interaction of neural populations at nearby locations which are *independently* tuned to different quantities.

Chapter 6 includes a general discussion of our research findings and future directions.

Chapter 2

Adaptation to visual numerosity changes neural numerosity selectivity

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Abstract

Perceiving numerosity, i.e. the set size of a group of items, is an evolutionarily preserved ability found in humans and animals. A useful method to infer the neural underpinnings of a given perceptual property is sensory adaptation. Like other primary perceptual attributes, numerosity is susceptible to adaptation. Recently, we have shown numerosity-selective neural populations with a topographic organization in the human brain. Here, we investigated whether numerosity adaptation can affect the numerosity selectivity of these populations using ultra-high field (7 Tesla) functional magnetic resonance imaging (fMRI). Participants viewed stimuli of changing numerosity (1 to 7 dots), which allowed the mapping of numerosity selectivity. We interleaved a low or high numerosity adapter stimulus with these mapping stimuli, repeatedly presenting 1 or 20 dots respectively to adapt the numerosity-selective neural populations. We analyzed the responses using custom-build population receptive field neural models of numerosity encoding and compared estimated numerosity preferences between adaptation conditions. We replicated our previous studies where we found several topographic maps of numerosity-selective responses. We found that overall, numerosity adaptation altered the preferred numerosities within the numerosity maps, resulting in predominantly attractive biases towards the numerosity of the adapter. The differential biases could be explained by the difference between the unadapted preferred numerosity and the numerosity of the adapter, with attractive biases being observed with higher difference. The results could link perceptual numerosity adaptation effects to changes in neural numerosity selectivity.

1. Introduction

The ability to process numerosity, i.e. the set size of a group of items, is an essential neurobiological feature found in humans from the moment of birth (Izard et al., 2009), and other species such as nonhuman primates (Nieder et al., 2002), birds (Scarf et al., 2011), amphibians (Krusche et al., 2010), fish (Miletto Petrazzini et al., 2016), and insects (Howard et al., 2018). Converging evidence from electrophysiology, psychophysics, and functional neuroimaging supports the existence of neural populations responding to specific numerosity ranges. More specifically, single-cell activity recordings in humans (Kutter et al., 2018), macaques (Nieder & Miller, 2003, 2004a; Viswanathan & Nieder, 2013), and crows (Wagener et al., 2018) have revealed neurons which respond selectively to low numerosities. The response amplitude of these neurons peaks when a specific numerosity is presented, i.e. the preferred numerosity, and decreases with the difference between the logarithm of the preferred numerosity and the presented numerosity.

Neural numerosity selectivity has also been examined using psychophysics and adaptation paradigms. Perceptual adaptation paradigms repeatedly present a particular stimulus (the adapter), which makes subsequently presented (reference) stimuli appear more different from the adapter than they are. Numerosity, similarly to other visual properties such as color or contrast, is susceptible to adaptation, yielding ‘repulsive’ aftereffects (see review by Anobile et al., 2016). Specifically, adaptation to a low numerosity leads to an overestimation of the numerosity subsequently presented in the adapted location, whereas adaption to a high numerosity leads to an underestimation (Burr et al., 2017; Burr & Ross, 2008). This perceptual repulsion from the adapter is often taken to demonstrate tuned neural responses to the adapted stimulus property because it is hypothesized to reduce the response amplitude of part of the neural tuning function, pushing the preferred stimulus state away from the adapter. Very low numerosities (as low as 3) can also be affected by adaptation, albeit with manipulation of attentional resources (Burr et al., 2011). Moreover, the aftereffects produced by adaptation to numerosity can occur even when using few trials and a brief presentation of the adapting numerosity stimulus (Aagten-Murphy & Burr, 2016; Tsouli, Dumoulin, et al., 2019; Tsouli, van der Smagt, et al., 2019).

Functional magnetic resonance imaging (fMRI) adaptation paradigms have also been used to elucidate neural selectivity to numerosity (Cantlon et al., 2006; Demeyere et al., 2014; Roggeman et al., 2011; Shuman & Kanwisher, 2004). This method takes advantage of the decreased blood-oxygenation-level-dependent (BOLD) responses associated with the repeated presentation of a specific stimulus, with responses recovering when a different stimulus is subsequently presented (Grill-Spector et al., 2006; Krekelberg, Boynton, et al., 2006; Larsson et al., 2016). For numerosity, the extent of this response recovery follows the numerical difference between the adapter and reference stimuli, suggesting neural tuning for numerosity (He et al., 2015; Jacob & Nieder, 2009; Kersey & Cantlon, 2017; Piazza et al., 2004). Furthermore, a study examining the effect of numerosity adaptation on numerosity decoding using fMRI and multi-voxel pattern analysis (MVPA) found less accurate (indeed chance level) classification of numerosities after adaptation when classifiers were trained on pre-adaptation data (Castaldi et al., 2016).

We have previously shown topographically organized neural populations tuned to numerosity, primarily located in and around the post-central sulcus in the superior parietal lobe, using ultra-high field (7 Tesla) fMRI and population receptive field (pRF) modeling (Harvey et al., 2013; Harvey & Dumoulin, 2017a). We further showed that the numerosity selectivity of these neural populations is relatively independent from non-numerical visual features (Harvey et al., 2015; Harvey & Dumoulin, 2017a, 2017b).

The goal of the present study was to examine whether the tuning of these numerosity selective neurons is systematically altered during perceptual adaptation following the repeated presentation of specific numerosities. Participants viewed stimuli of changing numerosity to map numerosity selectivity, as in our previous studies (control condition). In the experimental conditions, these numerosities were interleaved with a low numerosity (1 dot) or high numerosity (20 dots) adapter. We hypothesized that if neural populations' numerosity tuning is affected by adaptation, then their preferred numerosity would change depending on both the presence and the numerosity of the adapter.

2. Methods

2.1. Participants

We present data from eight human participants (five male, three female; age range 26-52 years). One was left-handed. All were well educated (postgraduate), with good mathematical abilities, and had normal or corrected-to-normal visual acuity. All gave written informed consent. All experimental procedures were approved by the ethics committee of University Medical Center Utrecht (protocol number 09/350).

2.2. Numerosity stimuli

The numerosity stimuli were presented on a 69.84 × 39.29 cm LCD screen (Cambridge Research Systems) positioned behind the MRI bore. Participants were required to lie still and view the display through a mirror attached to the head coil. The total distance from the attached mirror to the display screen was 220 cm and the display resolution was 1920 × 1080 pixels.

The stimuli were generated and presented using MATLAB (MathWorks, Inc.) and the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007). Similarly to the methodology used in our previous studies (Harvey et al., 2013; Harvey et al., 2015; Harvey & Dumoulin, 2017a,b), a large diagonal cross of thin red lines crossed the entire display, which facilitated accurate fixation at the cross intersection. The numerosity stimuli were groups of dots randomly positioned at each presentation so that all dots fell entirely within 0.75° (radius) of fixation. The random position of the dots ensured that the contrast energy was distributed similarly across the stimulus area for all numerosities. Moreover, the individual dots were distributed roughly homogeneously across the stimulus area to avoid perceptual grouping. We kept the total surface area of all of the dots combined constant across numerosities which ensured equal luminance across numerosities.

In all conditions, the numerosities 1 through 7 and 20 were presented as black dots on a gray background in 90% of dot presentations (including the adapter), while in the remaining 10%, the dots were shown in white (Figure 1a). Each numerosity stimulus was presented briefly (300 ms) to ensure participants did not have time to sequentially count the objects, at least in the case of higher numerosities (i.e. outside the subitizing range, > 4 items). The numerosity stimulus was then followed by an interstimulus interval (ISI) of 400 ms showing a uniform gray background. In the control condition, and for numerosities 1 through 7 (the 'main' stimuli for quantifying numerosity tuning), this was repeated six times over 4200 ms (three fMRI volume acquisitions, TRs) to produce strong fMRI responses and facilitate the measurement of response tuning (Figure 1b). Each of the main 1 through 7 numerosity stimuli was shown for a total of 48 times in each functional run. Each numerosity stimulus presentation contained a new random dot pattern, whether the numerosity changed or not.

In the low and high numerosity adaptation conditions, the main numerosity stimuli 1 through 7 were interleaved with a low (1 dot) and high (20 dots) numerosity adapter respectively (Figure 1a). More specifically, the main numerosity stimuli were first presented for 300 ms, followed by a 400 ms ISI, followed by the numerosity adapter for 300 ms, followed by another 400 ms ISI (Figure 1b). This was repeated three times over 4200 ms (three TRs). Therefore, the adapter was presented before and after the main numerosity stimuli during the stimulus sequence. Each of the main 1 through 7 numerosity stimuli was shown for a total of 24 times and the numerosity adapter for a total of 24 times in each functional run. This design kept the timing of the main numerosity stimuli the same for all conditions. The control condition can be seen as a special case where the adapter followed the numerosity of the main stimulus, changing to minimize systematic adaptation effects: in all conditions the main numerosity stimulus is likely to cause some adaptation as it contains repeated presentations of the same numerosity.

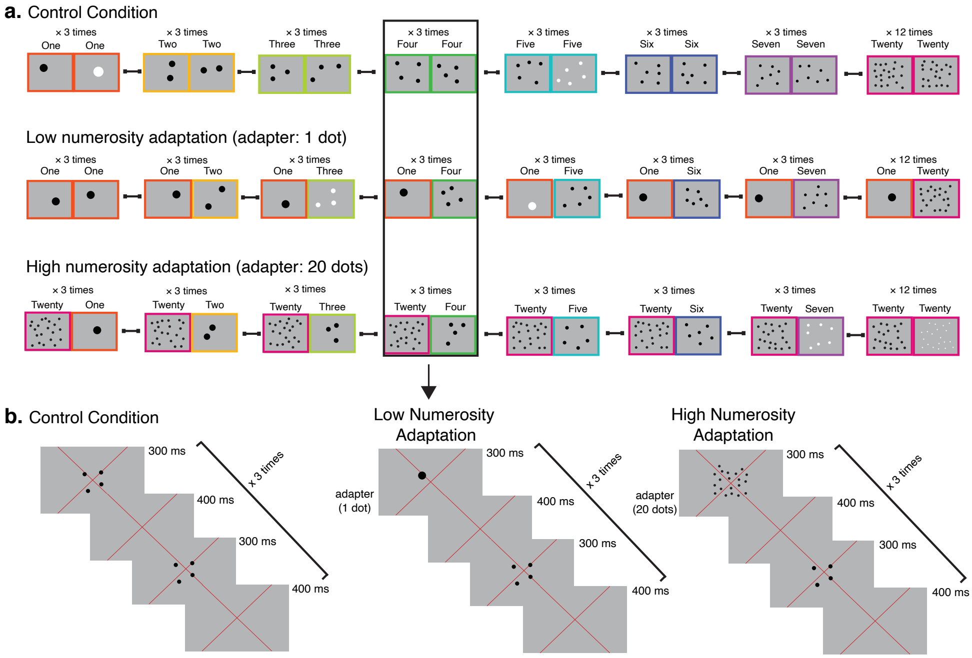

Figure 1. *Example of numerosity stimuli used (a) and schematic representation of stimuli presentation in each condition (b).* (a) In the control condition, numerosities 1 through 7 were the main numerosity stimuli, followed by a baseline of 20 dots. In the adaptation conditions, the main numerosity stimuli and baseline were interleaved with a low (1 dot) or high (20 dots) numerosity adapter. Therefore, the adapter was presented before and after the main numerosity stimuli during the stimulus sequence. (b) In the control condition, each of the main numerosity stimuli was shown six times before the numerosity changed, to ensure strong fMRI responses. In the adaptation conditions, the main numerosity stimuli and the adapter were shown three times before the numerosity changed, to ensure that changes in the main stimulus had the same timing in the adaptation conditions and control condition.

In all conditions, the main numerosity stimuli were first presented in ascending order, followed by a longer period (16.8 s) where the stimulus contained 20 dots, followed by the numerosities in descending order, followed by another long period of 20 dots. This sequence was repeated four times in each scanning run.

The long period of 20 dots served a relative "baseline" function, allowing us to distinguish neural populations with very small tuning widths which never responded to the main numerosities 1 through 7, and populations with very large tuning widths which always responded to these numerosities (Harvey et al., 2013). Thus, during this period, relatively little neural response was expected from neurons with lower numerosity preferences, because a numerosity of 20 dots should be well outside of the range that elicits strong responses. This allows hemodynamic responses to return back to baseline between blocks of changing numerosity. In the low and high numerosity adaptation conditions, the long period of 20 dots was also interleaved with the low (1 dot) and high (20 dots) numerosity adapter respectively, to maintain adaptation.

Participants were instructed to press a button when the dots were shown in white instead of black in order to ensure that they were paying attention to the stimuli during fMRI acquisition. No numerosity judgments were required.

2.3. Stimulus validation

Given the fast, sequential stimulus presentation and the rapid alternation between the main numerosity stimuli and the adapters in our fMRI paradigm, we evaluated whether our stimulus sequence does indeed yield repulsive aftereffects behaviorally (Aagten-Murphy & Burr, 2016; Tsouli, Dumoulin, et al., 2019; Tsouli, van der Smagt, et al., 2019). In the behavioral validation, we used the same numerosity adapters (1 and 20) and evaluated their effect on a reference stimulus of 10 dots, using a numerosity discrimination task (see Supplementary materials for more details). We used a reference stimulus of 10 dots since the behavioral detection of numerosity adaptation effects on very low numerosities (within the subitizing range) appears to require the introduction of an attention-demanding secondary task (Burr et al., 2011). We used the same presentation durations and interstimulus intervals as in our fMRI adaptation paradigm, and tested 10 participants, 6 of whom also participated in the fMRI experiment. We fitted the behavioral data with cumulative Gaussian functions to yield estimates of the point of subjective equality (PSE) which we used to illustrate the effect on numerosity adaptation on numerosity perception.

We found that, when compared to the control condition (no adaptation), there was a statistically significant increase in the perceived numerosity of the reference stimulus after adaptation to a low numerosity, and a statistically significant decrease in the perceived numerosity of the reference stimulus after adaptation to a high numerosity (Figure S2 in Supplementary materials). Thus, our behavioral experiment confirms that the stimulus sequence we used in our fMRI experiment is able to elicit repulsive perceptual aftereffects in behaviorally susceptible numerosity ranges.

2.4. FMRI acquisition

We acquired MRI data on a 7T Philips Achieva scanner. Similar acquisition protocols are described fully in our previous studies (Harvey et al., 2015; Harvey & Dumoulin, 2017a). Briefly, we acquired T1-weighted anatomical scans, automatically segmented these with Freesurfer (http://freesurfer.net), then manually edited labels to minimize segmentation errors using ITK-SNAP (http://www.itksnap.org/). This provided a highly accurate cortical surface model at the grey-white matter border to characterize cortical organization. Functional T2*-weighted 2D echo planar images were acquired using multiband acquisition (multiband factor: 2) and anterior-posterior encoding, and a 32-channel head coil, at a resolution of 1.77 × 1.77 × 1.75 mm, with a field of view of 227 × 227 × 70 mm. The TR was 1400 ms, echo time (TE) was 25 ms, and flip angle was 70°. Functional runs were each 273 time frames (382.2 s) in duration, of which the first 9 time frames (12.6 s) were discarded to ensure the signal was at steady state.

Three scanning sessions were required for each participant. In each scanning session, 3 functional runs were acquired for the control condition (9 runs in total, total duration: 57.33 min) and 3-4 runs for the adaptation conditions (10 runs for each adaptation condition in total, total duration: 63.70 min; with the exception of one participant where 9 runs were acquired for each condition due to technical issues). The additional run we acquired for the adaptation conditions was done to ensure strong fMRI responses, because the main numerosity stimuli were replaced with the adapters in half of presentations. The order of the conditions was counterbalanced across runs within and between participants. Moreover, in each session we acquired a top-up scan recorded with the opposite phase-encoding direction to correct for image distortion in the gradient encoding direction (Andersson et al., 2003).

2.5. Preprocessing of functional images

Co-registration of functional data to the high-resolution anatomical space were performed using AFNI (afni.nimh.nih.gov; Cox, 1996), which differs from our previous studies. A single transformation matrix was constructed, incorporating all the steps from the raw data to the cortical surface model to reduce the number of interpolation steps to one. No other spatial or temporal smoothing procedures were applied. A T1 image with the same resolution, position and orientation as the functional data was first used to determine the transformation to a higher resolution (1 mm isotropic) whole-brain T1 image (3dUnifize, 3dAllineate). For the fMRI data, we first applied motion correction to two series of images that were acquired using opposing gradient encoding directions (3dvolreg). Subsequently, we determined the distortion transformation between the average images of these two series (3dQwarp). We then determined the transformation in head position between and within functional scans (3dNwarpApply). Then we determined the transformation that co-registers this functional data to the T1 acquired in the same space (3dvolreg). We applied the product of all these transformations at every TR to transform our functional data to the whole-brain T1 anatomy. We repeated this for each fMRI session to transform all their data to the same anatomical space. We then imported these data into Vistasoft's mrVista framework (github.com/vistalab/vistasoft) for analysis and model fitting. For each adaptation condition, the time series of separate scans were averaged together, resulting in a very high signal-to-noise ratio.

2.6. FMRI data analysis

We estimated numerosity response models from fMRI data and stimulus time courses for each condition as previously described (Dumoulin & Wandell, 2008; Harvey et al., 2013, 2015; Harvey & Dumoulin, 2017a). The pRF model describes the aggregate tuning of the neural population within each fMRI recording site (voxel) using logarithmic Gaussian functions characterized by a preferred numerosity (mean of the Gaussian distribution) and a tuning width (standard deviation of the Gaussian in logarithmic numerosity space). A large set of candidate combinations of preferred numerosity and tuning width was generated.

At each gray matter voxel, the pRF model is estimated based on the fMRI data and the time course of numerosities presented within each TR. For each candidate preferred numerosity and tuning width, a predicted neural response time course is calculated as the amplitude of the candidate neural response function at each time point's presented numerosity. By convolving this predicted neural response time course with a hemodynamic response function (HRF), a predicted fMRI response time course is generated. For each fMRI recording site, the predicted fMRI response time course that most closely fits the recorded response time series course is chosen (by minimizing the sum of squared errors between the predicted and observed fMRI time series), giving the preferred numerosity and tuning width that generated that predicted fMRI response time course.

In the adaptation conditions, we fit models that include only the main numerosities, and models that include the main numerosities 1 through 7 and the presented adapter, and used the latter for subsequent analyses. However, in a general linear modeling framework (like a pRF model) these produce identical estimates of preferred numerosity and tuning width. Specifically, the adapter numerosity does not change through a scanning run, so it adds a constant component to the predicted response. FMRI data has an arbitrary baseline, so any constant component contributes to that baseline (which we do not analyze) without affecting other model parameters. We confirmed experimentally that pRF model parameters except baseline amplitude were identical whether we include or exclude the adapter state from the model's stimulus description. As a result of using this constant adapter, any changes in fMRI responses due to the presence of the adapter can only arise through non-linear interactions between response to the adapter and the main numerosity stimuli.

Candidate preferred numerosities extended beyond the presented numerosity range, allowing model fit parameters beyond this range. This meant that returned parameters within the 1 through 7 numerosity stimulus range were reported accurately, not just the best fit of a limited set. However, recording sites with preferences modeled outside the stimulus range must be treated with caution. In such recording sites, the response amplitude monotonically increases or decreases across the stimulus range. As such, we have little confidence that the preferred tuning estimate is correct. Therefore, recording sites whose preferred numerosity was outside the 1 through 7 range were excluded from further analysis.

Moreover, we excluded from further analysis the recording sites for which pRF models explained less than 27% of response variance (that is, those with a probability above 5% of observing this goodness of fit by chance). This threshold was calculated by fitting the numerosity models to the fMRI response time courses of white matter recording sites in the same scans for each participant. We then combined the numerosity models' fits from all participants' white matter to create a cumulative null distribution. The variance explained at the top 5% of that distribution (here, equivalent to 27% of response variance) was set as the threshold for all further gray matter analyses. Furthermore, and for all subsequent analyses, we selected recording sites for which pRF models explained more than 27% of response variance in the control condition alone. This meant that the selection of the recording sites were independent of their responses in the adaptation conditions.

2.7. Definition of regions of interest (ROIs)

We projected each recording site's preferred numerosity (estimated from the unadapted control condition) onto the inflated cortical surface for each condition. We defined region of interest (ROI) borders around numerosity maps showing a gradual change in numerosity preference, as previously described (Harvey & Dumoulin, 2017a).

In order to quantify changes in numerosity tuning between conditions, we examined the preferred numerosities of recording sites within each numerosity map and for each condition (control, low, and high numerosity adaptation). Specifically, we grouped the numerosity preferences of the recording sites in each numerosity map found in the left and right hemisphere across participants to create an aggregate pool of response data for each condition (control, low and high numerosity adaptation) in each numerosity map. We then selected the recording sites for which the pRF models explained more than 27% of response variance in the control condition. When comparing preferred numerosities between the control condition and either adaptation condition, we excluded recording sites with a preferred numerosity outside the presented numerosity range (1 through 7) in either compared condition.

In order to examine the effect of numerosity adaptation on neural numerosity preferences, we first calculated the change in preferred numerosity. For the low numerosity adaptation, we subtracted the preferred numerosity of recording sites in the low numerosity adaptation condition from the preferred numerosity of recording sites in the control condition. For the high numerosity adaptation, we subtracted the preferred numerosity of recording sites in the control condition from the preferred numerosity of recording sites in the high numerosity condition. Hence, in each adaptation condition, positive values indicate an attraction towards the numerosity of the adapter, and negative values indicate a repulsion from the numerosity of the adapter. We then binned the recording sites in each numerosity map into seven discrete numerosity categories (1 through 7) depending on their preferred numerosity in the control condition.

We also calculated the change in preferred numerosity by subtracting the preferred numerosity of recording sites in the control condition from the preferred numerosity of recording sites in each adaptation condition. Using this data representation, and in both adaptation conditions, positive versus negative values indicate a change in preferred numerosity towards higher versus lower preferred numerosities respectively, but each adapter induced a distinct effect (Figure S3 in Supplementary materials).

3. Results

3.1. FMRI response time courses and numerosity tuning functions change during adaptation

As illustrated in Figure 2, recorded fMRI response time courses at the same recording site differed in the three conditions (control, low numerosity adaptation, and high numerosity adaptation). The variance explained of the pRF models was lower in the adaptation conditions, as response amplitudes were lower. This is expected mainly due to less frequent presentation of the main (1 through 7) numerosity stimuli. The timing of responses also changed. The pRF models that best predict these responses capture these different responses as different preferred numerosity estimates in the three conditions.

3.2. Replication of network of numerosity maps

Numerosity maps were identified from the control condition (and clearly visible in the adaptation conditions) in the locations we have previously described (Harvey & Dumoulin, 2017a). NTO lay close to the temporo-occipital junction. NPO lay near the superior end of the parieto-occipital sulcus. NPC1, NPC2 and NPC3 lay in and around the parietal lobe's postcentral sulcus. NF lay at the junction of the precentral and superior frontal sulci. These locations were similar across participants (see Figure S4 and Table 1 in Supplementary materials).

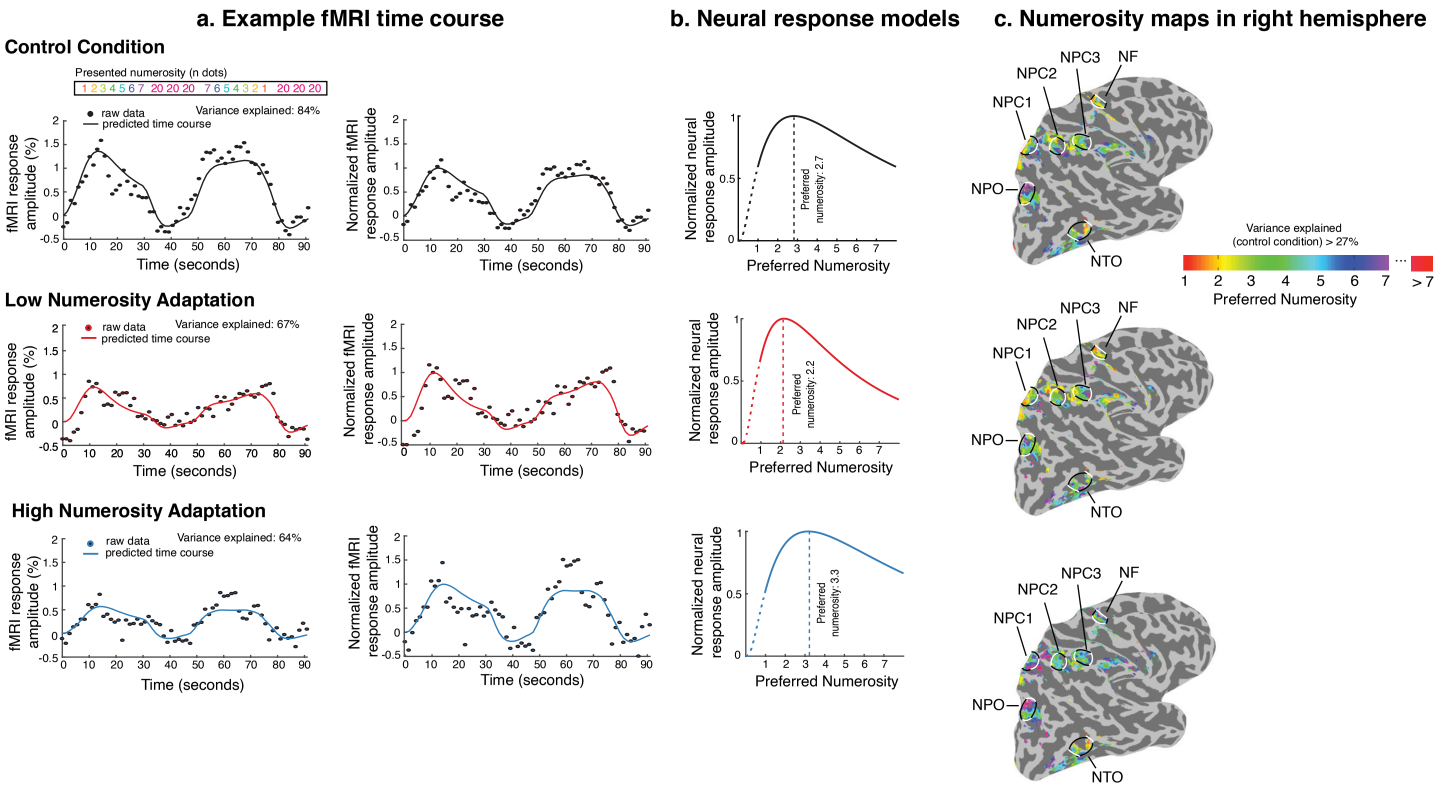

Figure 2. *Example fMRI time course (a), neural response models (b), and numerosity selective areas (c) in the right hemisphere of one participant.* (a) Example recorded fMRI time course from a single recording site (fMRI voxel) in the right posterior parietal cortex (NPC1) elicited by the numerosity stimulus sequence in the control (top), low numerosity adaptation (middle), and high numerosity adaptation condition (bottom). The points show the recorded fMRI time course, and the lines are the predicted fMRI time courses produced using pRF modeling in each condition. The largest response amplitude occurred after the presentation of low numerosities in this example, but its timing differed between conditions. (b) The pRF neural response models which give the best fitting predicted fMRI time series (shown in a). Each model describes a Gaussian tuning function in logarithmic numerosity space with two

parameters: a preferred numerosity and a tuning width defined by the full width at half maximum. In this example, preferred numerosity was biased towards a lower numerosity (2.2) during low numerosity adaptation compared to the control condition (2.7), and biased towards a higher numerosity (3.3) during high numerosity adaptation. (c) We found six topographic numerosity maps, i.e. extended areas where preferred numerosity changed gradually across the cortical surface. Colors show each recording site's preferred numerosity. White lines mark the borders of recording sites with the highest or lowest preferred numerosity present in each numerosity map. Black lines show borders of numerosity maps. Compared to the control condition, preferred numerosities within the numerosity maps were overall lower after low numerosity adaptation, and higher after high numerosity adaptation.

3.3. Preferred numerosity is altered by numerosity adaptation

As shown in Figure 3a, during adaptation to a low numerosity (1 dot), the preferred numerosities of neural populations in NPC1 were typically lower than in the control condition, whereas during adaptation to a high numerosity (20 dots), the preferred numerosities of neural populations in NPC1 were typically higher than in the control condition (Figure 3b).

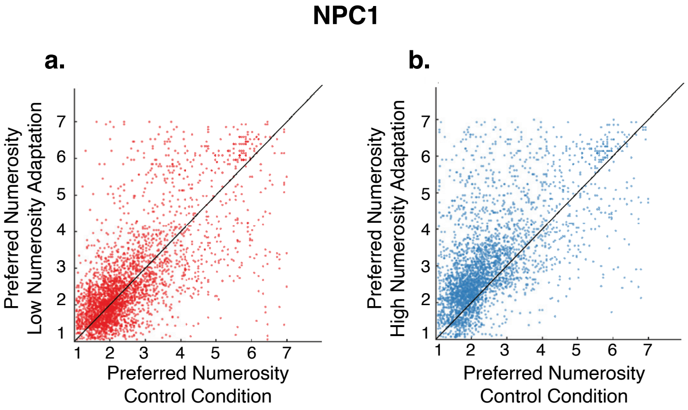

Figure 3. *Preferred numerosity of recording sites in NPC1 in the control vs. adaptation conditions.* The recording sites illustrated correspond to the aggregate pool of recording sites in the left- and right-hemisphere NPC1 of all participants. (a) The preferred numerosity of recording sites was typically lower than in the control condition during low numerosity adaptation. (b) The preferred numerosity of recording sites was typically higher than in the control condition during high numerosity adaptation.

3.4. Preferred numerosity changes as a function of the unadapted preferred numerosity

We found that after adaptation to a low numerosity, the higher range of preferred numerosities displayed attraction towards the numerosity of the adapter (1 dot), with the lower range of preferred numerosities displaying some repulsion from the numerosity of the adapter (Figure 4). After adaptation to a high numerosity, we found that the higher range of preferred numerosities displayed repulsion from the numerosity of the adapter (20 dots), while the lower range displayed attraction towards the numerosity of the adapter (Figure 4).

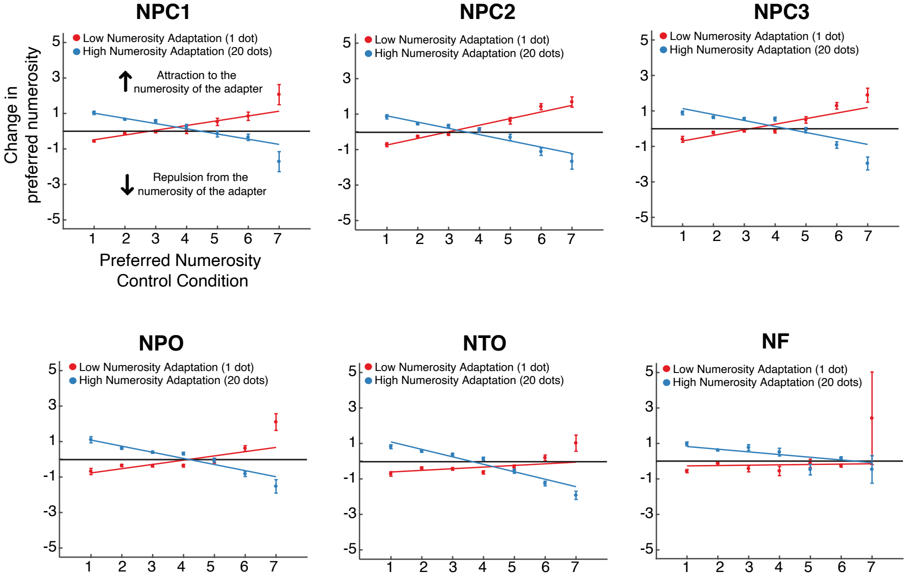

Figure 4. *Change in preferred numerosity after low (in red) and high (in blue) numerosity adaptation as a function of the unadapted preferred numerosity (control condition).* Each point represents the mean preferred numerosity in each numerosity bin and error bars correspond to the standard error of the mean (SEM). Positive values represent attraction to the numerosity of the adapter whereas negative values represent repulsion from the numerosity of the adapter in each adaptation condition. After low numerosity adaptation, the preferences of recording sites with higher preferred numerosities displayed attraction to the numerosity of the adapter (1 dot), with some repulsion for sites with lower preferred numerosities. Conversely, after high numerosity adaptation, the preferences of recording sites with lower preferred numerosities displayed attraction to the numerosity of the adapter (20 dots), and sites with higher preferred numerosities displayed repulsion.

3.5. Attraction of preferred numerosity towards the adapter numerosity increases with numerical distance from the adapter

The differential attractive or repulsive changes in preferred numerosity we found in each adaptation condition could be attributed to the difference between the preferred numerosity in the control condition and the numerosity of the adapter. Figure 5 illustrates the same data for NPC1 presented in Figure 4, which are now in logarithmic numerosity space, with the x axis showing the difference between the preferred numerosity in the control condition and the numerosity of the adapter in each adaptation condition, and the y axis showing the change in natural logarithmic preferred numerosity (see also Figure S5 in Supplementary materials for each numerosity map). The choice of a logarithmic scale allowed for more homoscedastic data, resulting in more accurate linear fits that we subsequently performed (though the obtained results were similar to those obtained from when using linear numerosity space). This representation shows more explicitly that the attraction of preferred numerosity increases when preferred numerosities are numerically further from the numerosity of the adapter in each adaptation condition.

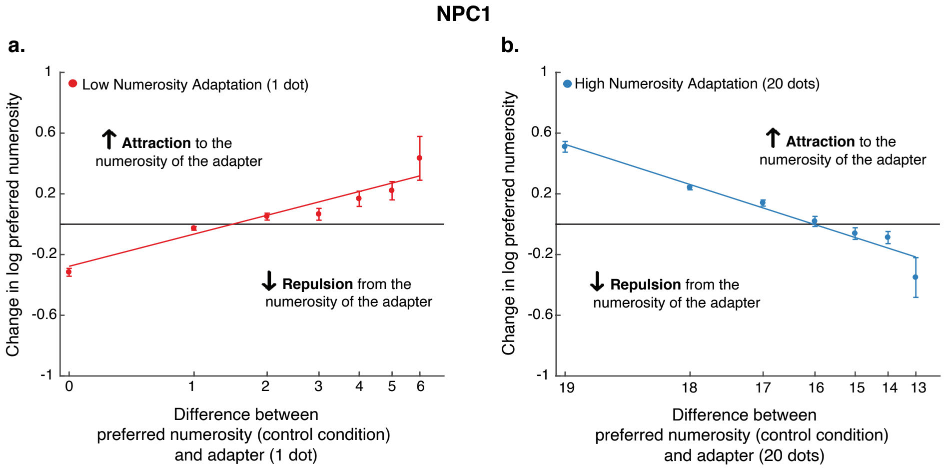

Figure 5. *Change in natural logarithmic preferred numerosity as a function of the difference between the preferred numerosity in the control condition and the numerosity of the adapter on a logarithmic scale.* Each point represents the mean preferred numerosity in each numerosity bin and error bars correspond to the SEM. When the preferred numerosity in the control condition is numerically closer to the numerosity of the adapter, preferred numerosities are repulsed from the numerosity of the adapter in each adaptation condition. However, when the preferred numerosity in the control condition is numerically further from the numerosity of the adapter, preferred numerosities are attracted to the numerosity of the adapter.

In order to further quantify the observed attraction to the numerosity of the adapter when preferred numerosities are numerically further from the numerosity of the adapter, we examined the change in natural logarithmic preferred numerosity as a function of the difference between the logarithmic preferred numerosity in the control condition and the logarithmic numerosity of the adapter. We did this for each adaptation condition, and for each numerosity map identified in each participant. Specifically, we first grouped the recording sites' data from the left- and right-hemisphere numerosity map of each participant. We then used a simple linear regression technique to fit the data of each numerosity map in each participant with a line and then used the slope of each regression line for subsequent analyses (Figure 6 and S6 in Supplementary materials for individual participants' data for each numerosity map).

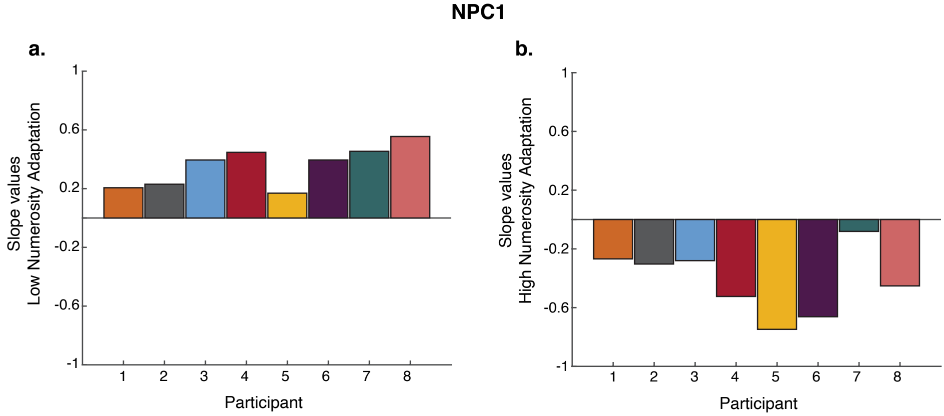

Figure 6. *Slope values of the change in logarithmic preferred numerosity for each participant in NPC1.* The slope values of each participant for each numerosity map were calculated using a simple linear regression method. (a) We found positive slope values in the low numerosity adaptation condition and (b) negative slope values in the high numerosity adaptation condition in all participants. This finding illustrates further the attraction to the numerosity of the adapter when preferred numerosities are numerically further from the numerosity of the adapter.

We then did a group-level analysis to examine whether the slope values in each adaptation condition and numerosity map were significantly different from zero across participants (Figure 7). We conducted a series of one-sample *t*-tests, after ensuring that the normality assumption was not violated by conducting a series of the Shapiro–Wilk tests ($p > 0.05$ for each variable), and used false discovery rate (FDR)-corrected significance thresholds.

When examining the mean slope values for the low numerosity adaptation condition, we found that they were significantly different from zero and this difference was statistically significant in all numerosity maps (NPC1: Mean = 0.36, *SE* = 0.05, *t*(7) = 7.29, *p* = 0.001; NPC2: Mean = 0.34, *SE* = 0.04, *t*(7) = 7.72, *p* = 0.001; NPC3: Mean = 0.29, *SE* = 0.05, *t*(7) = 5.58, *p* = 0.001; NPO: Mean = 0.35, *SE* = 0.05, *t*(7) = 7.51, *p* = 0.001; NTO: Mean = 0.23, *SE* = 0.07, *t*(6) = 3.41, *p* = 0.014; NF: Mean = 0.57, *SE* = 0.12, *t*(7) = 4.55, *p* = 0.003, FDR-corrected significance thresholds).

The same pattern was found in the high numerosity adaptation condition, where the mean slope values were significantly different from zero and this difference was statistically significant in all numerosity maps (NPC1: Mean = -0.41, *SE* = 0.08, *t*(7) = -5.25, p = 0.002; NPC2: Mean = -0.45, *SE* = 0.08, *t*(7) = -5.61, *p* = 0.001; NPC3: Mean = -0.39, *SE* = 0.04, *t*(7) = -9.10, *p* = 0.001; NPO: Mean = -0.44, *SE* = 0.07, *t*(7) = -6.64, *p* = 0.001; NTO: Mean = -0.36, *SE* = 0.06, *t*(6) = -5.63, *p* = 0.002; NF: Mean = -0.62, *SE* = 0.12, *t*(7) = -5.10, *p* = 0.002, FDR-corrected significance thresholds).

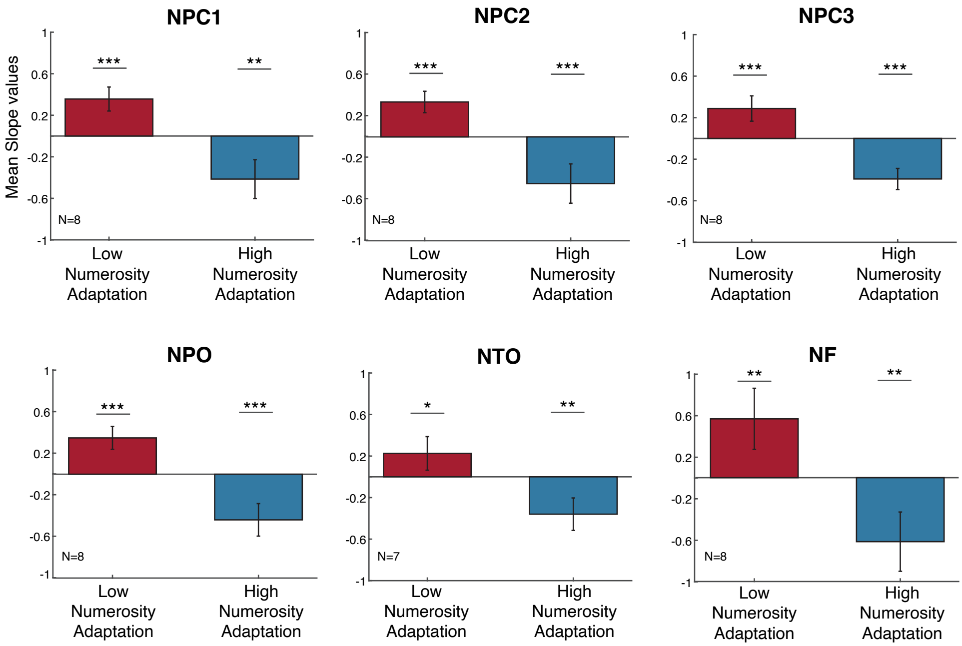

Figure 7. *Mean slope values of the change in logarithmic preferred numerosity in each numerosity map and adaptation condition across participants*. The error bars correspond to the 95% confidence intervals of the mean slope values, and asterisks denote the level of statistical significance of the one-sample *t*-tests (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, FDR-corrected). N corresponds to the number of participants in which each map was identified. In all adaptation conditions and numerosity maps, we found that the mean slope values were statistically different from zero, further validating the finding that preferred numerosity is attracted to the numerosity of the adapter when they are numerically further from each other.

Furthermore, we obtained the same results when analyzing the slope values in each adaptation condition separately for the left- and right-hemisphere numerosity maps (Figure S7 in Supplementary materials).

We also tested whether the slope values in each adaptation condition were significantly different from zero across the numerosity maps identified in each participant (see Supplementary materials). We conducted a series of one-sample *t*-tests and found that in all participants and adaptation conditions, the mean slope values were statistically different from zero, further validating the finding that preferred numerosity is attracted to the numerosity of the adapter when they are numerically further from each other (Figure S8 in Supplementary materials).

4. Discussion

The goal of the present study was to examine whether and how the numerosity tuning of human neural populations changes during numerosity adaptation. We displayed visual stimuli of changing numerosity (1 through 7) which were interleaved with a low (1 dot) or high (20 dots) numerosity adapter while collecting ultra-high field (7T) fMRI data. Using a pRF modeling approach, we quantified the preferred numerosity of neural populations during low and high numerosity adaptation and compared this to the preferred numerosity in an unadapted control condition. We focused on populations within six recently described topographic numerosity maps (Harvey & Dumoulin, 2017a). We found that numerosity preferences within each numerosity map decreased during low numerosity adaptation and increased during high numerosity adaptation, indicating that preferred numerosities were predominantly attracted to the numerosity of the adapter. However, when adapted to numerosity 1, recording sites with preferred numerosities between 1 and 2 were (slightly) repelled from the adapted numerosity, and so were the recording sites with preferred numerosities between 6 and 7 when adapted to numerosity 20.

In an effort to disentangle the attractive versus repulsive biases observed in each adaptation condition, we found that the observed biases could be explained in terms of the numerical distance of the unadapted preferred numerosities (control condition) from the numerosity of the adapter. Specifically, we found that preferred numerosities were attracted to the numerosity of the adapter when they were numerically further from the adapter in each adaptation condition. This effect of adaptation was markedly similar in all six numerosity maps found in our study. This is particularly striking given the generally wide structural separation of these areas across the cortical surface, and further reinforces the notion that these numerosity selective neural populations are part of a cohesive numerosity-processing network (Harvey & Dumoulin, 2017a). Specifically, it is possible that the different numerosity maps work in parallel to analyze different aspects of numerical information, similarly to how sensory maps operate (Young, 1998). Interestingly, the location of the maps includes areas implicated in a variety of perceptual and cognitive functions, among which are attentional control, decision-making, mathematics as well as visual motion, object processing and object recognition (Harvey & Dumoulin, 2017a). Furthermore, the NPC maps we find in the postcentral sulcus could be homologues to the numerosity-selective neural populations identified on the fundus of the macaque intraparietal sulcus (Harvey et al., 2017; Nieder & Miller, 2004a). Nevertheless, the causal role of these numerosity maps in numerical cognition remains to be established.

An fMRI study by Piazza et al. (2004), examining parietal responses to number change using a numerosity repetition suppression paradigm, found suppression of responses when the adapter and test stimuli were numerically close (e.g. both being 16 items), and recovery of responses when the test stimuli were 50% (8 items) or 200% (32 items) of the adapter (16 items). A similar effect was found by an fMRI repetition suppression study from Jacob and Nieder (2009), examining neural population tuning to preferred proportions (i.e. not absolute numerosity), where recovery from BOLD signal adaptation increased as the numerical distance between the adaptation and deviant proportions grew larger. In regard to our finding on the repulsion of preferred numerosity away from the adapter numerosity when they are numerically closer, it could be suggested that the response suppression reported by Piazza et al. (2004) and Jacob and Nieder (2009) could result in a repulsive change in preferred numerosity similar to the one we report here. Specifically, if part of the neural response function nearer the adapter numerosity is suppressed more than the part of the response function further away, the numerosity producing the largest response (the preferred numerosity) will move away from the adapter.

The overall attraction of neural numerosity tuning to the numerosity of the adapter is seemingly at odds with the repulsive aftereffects on numerosity perception during numerosity adaptation (Aagten-Murphy & Burr, 2016; Burr et al., 2011; Burr & Ross, 2008). However, we argue that the attractive biases on a neural level could potentially yield repulsive effects on perception. To give an illustrative example, adaptation to a numerosity of 1 might attract the unadapted preferred numerosity of a neural population from 5 to an adapted preferred numerosity of 4. Then, when 4 is presented, it will yield a maximal neural response in that population, while normally that maximal response would occur for 5. In this way, the pattern of neural activity normally associated with 5 occurs for 4, so 4 may be perceived as 5, a repulsive effect on perception.

Such links between attraction of neural response preferences and repulsion of perception have been described before. Kohn and Movshon (2004) examined how macaque MT motion direction tuning changes during motion direction adaptation. They modeled the response of the MT cell population in order to predict how the population response and thus, the perceived motion direction, would shift after adaptation. Their model showed that attractive shifts in single-cell tuning predict a repulsive perceptual aftereffect consistent with those measured psychophysically. We have previously shown that population receptive fields are attracted towards the focus of attention (Klein et al., 2014). Modeling these effects demonstrated that stimuli located near the focus of attention stimulate receptive fields that are positioned further away in the absence of attention (Klein et al., 2016). The perceived position of these stimuli shifts the stimulus away from the attended location, while population receptive fields shift towards the attended location.

Another possibility is that our stimulus could produce serial dependence rather than classical adaptation effects, yielding attraction rather than repulsion of perceived numerosity. Serial dependence attracts the perception of numerosity to the immediately preceding numerosity and operates over short timescales (Cicchini et al., 2014; Corbett et al., 2011; Fornaciai & Park, 2018). By conducting a validation experiment with our stimulus, we found evidence for repulsion (not attraction) of numerosity perception. This is in agreement with other psychophysical studies on numerosity adaptation using brief adapter presentation (Aagten-Murphy & Burr, 2016; Tsouli, Dumoulin, et al., 2019; Tsouli, van der Smagt, et al., 2019). We are therefore confident that our adaptation sequence repels numerosity while attracting neural numerosity preferences.

As we note in the Methods, our stimulus sequence presented the same numerosity repeatedly and frequently (every 700 ms) and moved through numerosities gradually and sequentially (every 4200 ms), as in our previous experiments. This repeated presentation and gradual change are likely to cause some repetition suppression of responses to each stimulus display, and perhaps perceptual adaptation to the changing numerosity as well as the adaptors. First, while repetition suppression will reduce the responses to each display, presenting each numerosity only once before moving on would almost certainly produce a smaller response and less clear results. Second, given the slowness of the hemodynamic response and resulting poor temporal resolution of fMRI, changing numerosity on every display would prevent us from separating responses to different numerosities in the resulting fMRI time course (if presented at the same rate) or would require a few seconds between displays, and therefore far more scanning. These design choices greatly increase the efficiency of our method to quantify numerosity selectivity using fMRI.

But how do these factors affect our estimates of preferred numerosity? First, changing numerosities slowly and sequentially makes the preferred numerosity estimates less sensitive to the precise timing of the modelled hemodynamic response function: small deviations from the modelled timing only slightly change which numerosity was being presented at the time of any modelled neural response. Second, we do not expect repeated presentations and slow, sequential changes to systematically affect preferred numerosity estimates. Repetition suppression of responses from the same numerosity should not change which part of the response function is responding, only reduce its amplitude. A preceding presentation of a different numerosity is likely to affect the preferred numerosity estimate, but by using “sweeps” in both ascending and descending directions for the same model we aim to balance opposing effects of preceding lower and higher numerosities. Given that we find that the adaptation’s neural effects increase with distance between the adapter’s numerosity and the population’s preferred numerosity, keeping preceding numerosities as close as possible to the current presentation should also minimize effects of preferred numerosity estimates. Finally, it is likely that participants know which numerosity to expect in each display, as this is highly predictable. It is less clear how expectation might affect numerosity selectivity, but we would expect a global increase or decrease in response amplitude and we have no reason to expect a systematic bias would result from expectation. Importantly, all of the effects described above should affect the responses to both adaptation conditions similarly, so seem unlikely to explain the differences we see between conditions.

Our results further illustrate that the preferred numerosity of neural populations with numerosity preferences in the subitizing range (less than 4, allowing fast and error-free numerosity judgements) can be affected by adaptation. The majority of psychophysical studies on numerosity adaptation (Aagten-Murphy & Burr, 2016; Anobile, Cicchini, et al., 2018; Burr & Ross, 2008; Liu et al., 2017; Tsouli, Dumoulin, et al., 2019; Tsouli, van der Smagt, et al., 2019) report effects on perception of higher numerosities (typically ≥ 9 items). Only one behavioral study has shown adaptation effects on perception of numerosities within the subitizing range, and only under conditions of high attentional load induced by a secondary task (Burr et al., 2011). Here, we show that neural numerosity tuning within the subitizing range can be altered by numerosity adaptation even in the absence of attentional load. Nevertheless, it is possible that this change in neural tuning for numerosities within the subitizing range might be too subtle to affect numerosity perception when measured psychophysically.

5. Conclusions

Using a numerosity adaptation paradigm combined with ultra-high field fMRI and a pRF modeling approach, we show that neural numerosity selectivity was altered systematically in all numerosity maps. Specifically, neural numerosity preferences were overall attracted to the numerosity of the adapter, with the extent of attraction increasing when the unadapted preferred numerosities were numerically further from the numerosity of the adapter. We argue that these attractive biases could potentially underlie the perceptual effects of numerosity adaptation.

Chapter 3

Adaptation reveals unbalanced interaction between numerosity and time

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Abstract

Processing quantities such as the number of objects in a set, size, spatial arrangement and time is an essential means of structuring the external world and preparing for action. The theory of magnitude suggests that number and time, among other continuous magnitudes, are linked by a common cortical metric, and their specialization develops from a single magnitude system. In order to investigate potentially shared neural mechanisms underlying numerosity and time processing, we used visual adaptation, a method which can reveal the existence of a dedicated processing system. We reasoned that cross-adaptation between numerosity and duration would concur with the existence of a common processing mechanism, whereas the absence of cross-adaptation would provide evidence against it. We conducted four experiments using a rapid adaptation protocol where participants adapted to either visual numerosity or visual duration and subsequently performed a numerosity or duration discrimination task. We found that adapting to a low numerosity altered the estimation of the reference numerosity by an average of 5 dots, compared to adapting to a high numerosity. Similarly, adapting to a short duration altered the estimation of the reference duration by an average of 43 msec, compared to adapting to a long duration. In the cross-dimensional adaptation conditions, duration adaptation altered numerosity estimation by an average of 1 dot, whereas there was not sufficient evidence to either support or reject the effect of numerosity adaptation on duration judgments. These results highlight that there are partially overlapping neural mechanisms which are dedicated for processing both numerosity and time.

1. Introduction

Our ability to distinguish between stimuli that differ in numerosity, the number of objects in a set, is an evolutionary pivotal trait identified in humans from early developmental stages (Barth et al., 2005; Schleger et al., 2014; Xu & Spelke, 2000), and shared by many non-human species (Cantlon & Brannon, 2007; Ditz & Nieder, 2016; Jones et al., 2014; Miletto et al., 2016). This apparent innate sense of number is implicated in the development of complex mathematical abilities (see meta-analyses by Schneider et al., 2017; Schwenk et al., 2017). However, it is currently debated whether numerosity is a primary sensory property processed by dedicated neural mechanisms, or whether it is part of a unified magnitude system which processes all kinds of quantity information (Kadosh et al., 2008; Leibovich et al., 2017). Similarly, the existence of a dedicated system for time perception remains elusive, with some studies demonstrating that temporal processing relies on specialized neural networks (see reviews by Grondin, 2010; Ivry & Schlerf, 2008), and others showing that time is strongly associated with numerosity as part of a generalized magnitude system (de Hevia et al., 2014; Lourenco & Longo, 2010).

An influential theoretical framework accounting for the abovementioned findings is the "A Theory Of Magnitude" (ATOM) proposed by Walsh (2003; Bueti & Walsh, 2009). According to this theory, the specializations for number, time and space processing develop from a single magnitude system. Indeed, a number of studies support the existence of shared processing mechanisms between numerosity, time and space (Cai & Connell, 2015; Hubbard et al., 2005; Schwiedrzik et al., 2016; Srinivasan & Carey, 2010).

Most of the evidence supporting ATOM come from neuroimaging studies which show that numerosity and duration processing rely on spatially overlapping cortical systems (Dormal, Andres, et al., 2012; Hayashi, Kanai, et al., 2013; Hayashi et al., 2015; Skagerlund et al., 2016). However, the overlapping activations do not necessarily imply overlapping mechanisms. Moreover, these studies use distinct tasks for evaluating numerosity and duration discrimination, a method which does not allow robust conclusions on whether numerosity and duration truly interact. There are a few behavioral studies which employ a cross-dimensional paradigm and use non-symbolic numerosities but have yielded conflicting findings, showing either a unidirectional interference of numerosity on duration judgments (Alards-Tomalin et al., 2016; Dormal et al., 2006), or a unidirectional influence of duration on numerosity (Lambrechts et al., 2013; Martin et al., 2017). Conversely, Javadi and Aichelburg (2012) found a bidirectional interference, while Agrillo, Ranpura and Butterworth (2010) found no interference.

A powerful psychophysical tool which can further elucidate whether numerosity and time rely on similar neural networks as ATOM postulates, is perceptual adaptation. Adaptation has been described as the “psychophysicist’s microelectrode” (Frisby, 1979), since the visual aftereffects produced after adapting to a stimulus isolate the neural networks which respond selectively to the features of that stimulus, offering a behavioral window in the underlying cortical processes (Blake & He, 2005; Thompson & Burr, 2009). Both numerosity and duration perception adapt (Burr & Ross, 2008; Heron, Aaen-Stockdale, et al., 2012; Heron, Roach, et al., 2012). Adapting to a low numerosity leads to an overestimation of the numerosity subsequently presented in the adapted location, whereas adapting to a high numerosity leads to an underestimation (Aagten-Murphy & Burr, 2016; Anobile et al., 2014, 2015, 2016). Moreover, adaptation to numerosity can occur across sensory modalities and across presentation formats, supporting the existence of an abstract quantity system (Arrighi et al., 2014). Similarly, adaptation to a short and long auditory or visual duration induces expansion and contraction of subsequently heard or viewed durations respectively (Heron et al., 2013). However, and contrary to numerosity adaptation, the spatial selectivity of visual duration adaptation remains unclear (Heron, Roach, et al., 2012; Johnston et al., 2006; Li et al., 2015; Maarseveen et al., 2017).

Here, we investigate the presence of a common perceptual system underlying numerical and temporal processing using cross-dimensional visual adaptation. More specifically, we examined whether adapting to numerosity can alter duration perception and vice versa. We hypothesized that if numerosity and time perception rely on shared processing networks, then adaptation to visual numerosity should affect duration discrimination, and adaptation to visual duration should affect numerosity discrimination.

2. Materials and methods

2.1. Participants

Twenty participants completed the experiment (8 female, 12 male). All subjects had normal or corrected-to-normal visual acuity and were naïve to the purpose of the study. Three authors (AT, StP, MvdS) also did the experiment and their results corroborated the results of the naïve subjects but were excluded from the final analysis since they were aware of the hypotheses of the study. One additional participant was also excluded because of misunderstanding the experiment’s instructions. Participants gave written informed consent and received a monetary reward or course credits. The experiment was conducted in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Faculty of Social and Behavioural Sciences of Utrecht University.

2.2. Apparatus and stimuli

Participants sat at about 60 cm distance from a 60 × 34 cm, Asus liquid crystal display (LCD) monitor with 2560 × 1440 resolution and a refresh rate of 60 Hz. The display was linearized using a photometer (Mavo Monitor USB, Gossen, Nürnberg, Germany). The stimuli (viewed binocularly) were circular patches containing an equal proportion of black and white dots displayed on a mean luminance background (60 cd/m^2) at 80% Michelson contrast. Each dot had a diameter of .2° of visual angle and the circular patches had a diameter of 12°. In each trial, dots were scattered randomly within the circular patches and were not allowed to overlap.

In numerosity adaptation, the adapters were circular patches of 20 or 80 dots, while the reference was a patch of 40 dots (Figure 1a). The numerosity of the test patch varied from trial to trial using the Minimum Expected Entropy staircase method (Saunders & Backus, 2006). In duration adaptation, the adapters were circular patches of 40 dots presented for either 67 msec or 600 msec, while the reference was a patch of 40 dots lasting for 333 msec. The test stimuli were bursts of white noise (70 dB) presented binaurally through Sennheiser HD201 headphones and their duration varied using the aforementioned staircase method (Maarseveen et al., 2017). The numerosity adapters (20 vs 80 dots) were chosen to produce strong and repulsive adaptation aftereffects on the reference numerosity of 40 dots. Likewise, the duration adapters (67 vs 600 msec) were chosen to produce strong and repulsive adaptation aftereffects on the reference duration of 333 msec. Thus, we ensured significant adaptation aftereffects on the unidimensional adaptation conditions, which were a prerequisite for the cross-dimensional adaptation conditions. Furthermore, the adapters used are in line with other studies on numerosity (Aagten-Murphy & Burr, 2016; Castaldi et al., 2016; Turi et al., 2015) and duration adaptation (Heron, Aaen-Stockdale, et al., 2012; Heron et al., 2013; Maarseveen et al., 2017). Moreover, our choice of a visual reference stimulus and an auditory test stimulus was based the suggestion that duration adaptation is not spatially selective (Li et al., 2015; Maarseveen et al., 2017), contrary to numerosity adaptation (Burr & Ross, 2008). Hence, adapting to a visual duration would produce perceptual aftereffects on the same side as the adapter and on the opposite side. In addition, using an auditory test stimulus instead of a visual one is in line with previous studies on duration adaptation (Heron, Aaen-Stockdale, et al., 2012; Maarseveen et al., 2017).

All stimuli were generated and presented using MATLAB 2016b (MathWorks, Inc.) and the Psychophysics Toolbox 3.0.13 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

In numerosity adaptation, subjects first performed the neutral adaptation condition (40 dots), and then adapted to a low (20) or high (80) numerosity (see Figure 1b for a schematic illustration of a single trial). The center of the dot patches was at 8° eccentricity left of fixation for the first half of the trials and right of fixation for the other half (100 trials in total), with the "side"-block also being counterbalanced across participants. The reference patch (40) appeared at the adapted location and the test patch at the opposite side. We used a rapid adaptation paradigm similar to Aagten-Murphy and Burr (2016), where the adapter was presented for 333 msec with no top-up adaptation. After a 300 msec pause, the reference patch was presented for 333 msec, followed by another 300 msec pause and then the test patch appeared for 333 msec. Using the two-alternative forced-choice (2AFC) paradigm, participants were asked to respond as accurately as possible (guessing if unsure) which of the two patches, the reference or the test, appeared to have more dots by pressing the appropriate key. After responding, the next trial started after 500 msec.

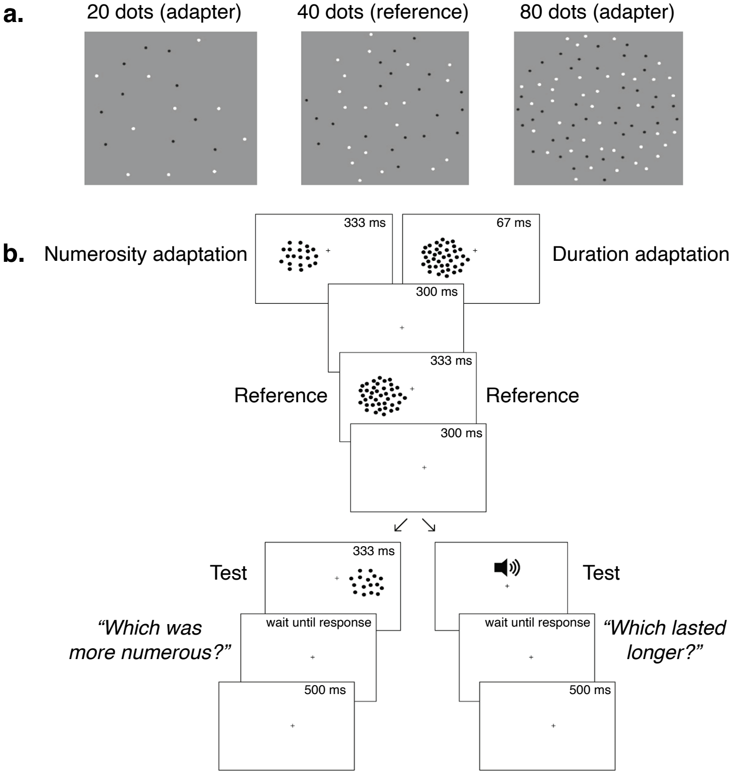

Figure 1. *Illustration of the stimuli and procedures*. (a) The adapters and reference used for numerosity and duration adaptation (note that the dots were not overlapping and their position within the circular patch was random in every trial). (b) Schematic illustration of a single trial in each adaptation-task condition. In numerosity adaptation, a low (20 dots) or high (80 dots) numerosity adapter would be presented either to the left or the right of the fixation cross. The reference numerosity (40 dots) was presented at the adapted location, and the test (varying in numerosity) was presented at the opposite side. The same design was followed in the duration adaptation-numerosity discrimination condition, with the only change being a 40-dots adapter lasting for 67 msec (short) or 600 msec (long). In duration adaptation, a short or long duration adapter of 40 dots would be presented either to the left or the right of the fixation cross. The reference was a 40-dot patch (333 msec) presented at the adapted location. The test (white noise of varying duration) was presented binaurally via headphones. In the numerosity adaptation-duration discrimination condition, the same design was followed, with the only change being a low or high numerosity adapter presented for 333 msec.

In duration adaptation, we used a modified version of the duration adaptation method by Heron, Aaen-Stockdale, et al. (2012), and applied the same, rapid adaptation protocol we used for numerosity adaptation (Figure 1b). Subjects first performed the neutral adaptation condition (40-dot patch; 333 msec) and then adapted to a short (67 msec) or a long (600 msec) duration. The reference was a 40-dot patch (333 msec) presented in the adapted location, while the test was an auditory burst of white noise of varying duration. Participants were asked to respond using a 2AFC paradigm whether the reference or the test lasted longer by pressing the appropriate key.

The same procedure was followed in the cross-dimensional adaptation conditions, with subjects being adapted to a low or high numerosity and tested on duration discrimination and adapted to a short or long duration and tested on numerosity discrimination (Figure 1b). The order of the magnitude of adaptation (low/high numerosity; short/long duration) was counterbalanced within and across participants. Moreover, in order to avoid carry-over effects, participants were adapted to numerosity/duration and tested on the numerosity discrimination task on one day and adapted to duration/numerosity and tested on the duration discrimination task the following day, with the order of the task (numerosity or duration discrimination) being, again, counterbalanced across participants.

2.3. Data analysis

All data analyses were conducted using MATLAB, SPSS (version 24.0, SPSS Inc., Chicago, IL, USA) and JASP (version 0.8.1.2, JASP Team, 2017; jasp-stats.org). After the experiment, we ordered the data by adding the values obtained per side block (left vs right presentation side), sorting them on test numerosity or test duration and subsequently creating 10 equally sized bins of 10 trials. We then fitted these data with cumulative Gaussian functions to yield estimates of the point of subjective equality (PSE) and slope for each condition and used the PSE and slope values for subsequent analyses on the effects of numerosity and duration adaptation.

Given that adaptation stimuli were presented at one side (e.g., left) for half trials and at the opposite side (e.g., right) for the other half, we wanted to ensure that this design would not yield significant differences in the average PSE and slope values. Indeed, there were no statistically significant differences in the obtained measurements when the adaptation stimuli were presented to the left compared to the right side in each adaptation condition-task, after using false discovery rate (FDR)-corrected significance thresholds. Likewise, there were no statistically significant main or interaction effects of the presentation side block (adaptation trials starting from the left or right side) and task order (performing the numerosity discrimination tasks at day 1 and the duration discrimination tasks at day 2, and vice versa) on average PSE values in each adaptation condition-task using FDR-corrected significance thresholds.

3. Results

Figure 2 demonstrates the shift in the psychometric curves of a single subject depending on the magnitude of the adapter, after plotting the proportion of trials where the test was perceived as more numerous or longer in duration than the reference (40 dots; 333 msec).

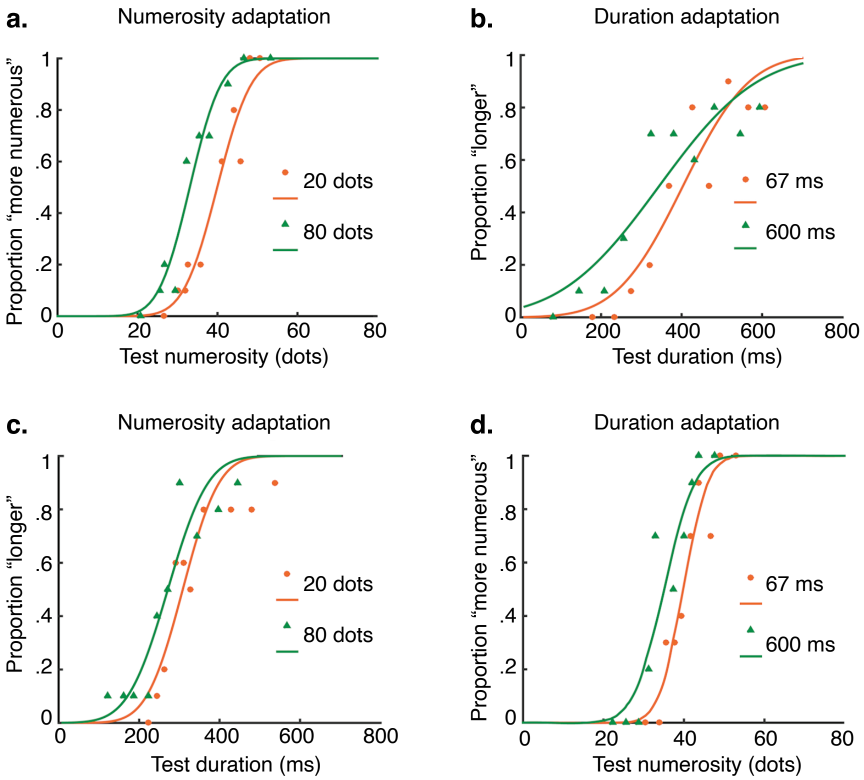

Figure 2. *Psychometric curves of a single subject.* (a) Adaptation to a low numerosity resulted in an overestimation of the reference numerosity, and adaptation to a high numerosity resulted in an underestimation of the reference numerosity. (b) Similarly, adaptation to a short and long duration resulted in an overestimation and underestimation of the reference duration respectively. (c) In the cross-dimensional adaptation conditions, adaptation to a low and high numerosity resulted in an overestimation and underestimation of the reference duration respectively, (d) whereas adaptation to a short and long duration resulted in an overestimation and underestimation of the reference numerosity respectively.

There were no outliers and the average PSE values in each adaptation condition-task were normally distributed, as assessed by boxplot and the Shapiro–Wilk test ($p > .05$). A series of two-tailed, paired-samples t-tests were conducted to examine whether average PSE values in numerosity and duration discrimination tasks were significantly different after adapting to a low and high numerosity, and a short and long duration. The p values obtained were FDR-corrected for multiple comparisons where applicable, and the reported Cohen's d effect sizes were corrected for dependence between means (Morris & DeShon, 2002).

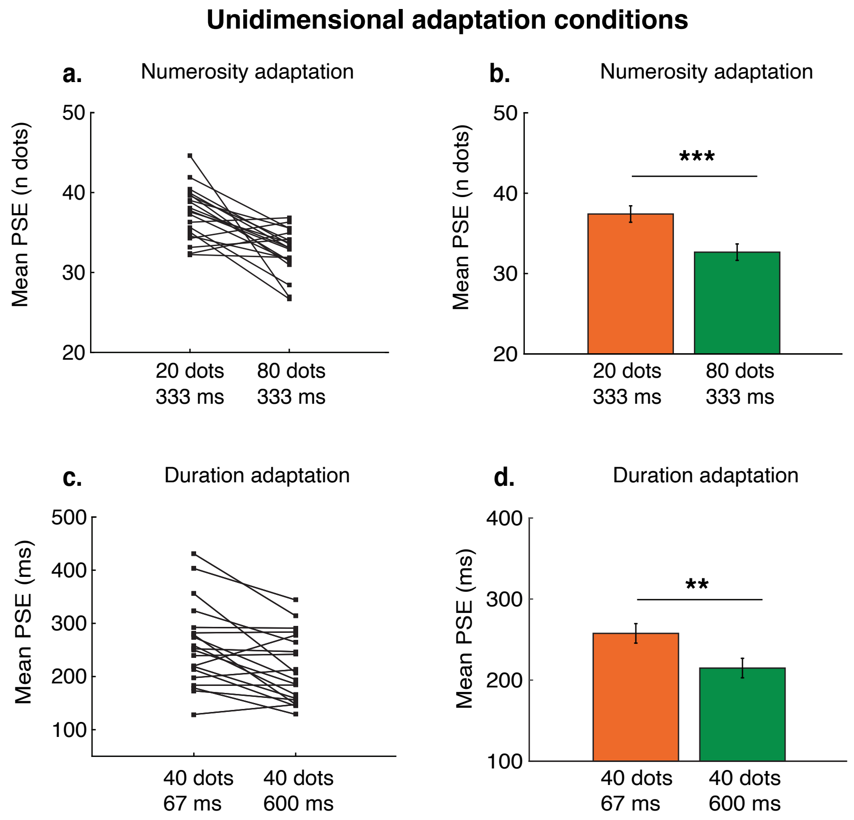

Figure 3. *PSE values in the unidimensional adaptation conditions per participant (left) and on a group level (right)*. (b) On a group level, numerosity discrimination was significantly affected by numerosity adaptation, (d) and duration discrimination was significantly affected by duration adaptation. Error bars represent 95% Confidence Intervals, adjusted for a within-subjects design (Loftus & Masson, 1994).

In numerosity adaptation (Figure 3b), the mean PSE values in the numerosity discrimination task were significantly higher after adaptation to a low numerosity (20 dots; *M* = 37.41 dots, *SD* = 3.25) compared to a high numerosity (80 dots; *M* = 32.66 dots, *SD* = 2.84 dots), *t*(19) = 4.57, *p* < .001, Cohen's *d* = 1.02. These data were also examined by estimating a Bayes factor using Bayesian Information Criteria (Jarosz & Wiley, 2014, p.6; Wagenmakers, 2007), comparing the fit of the data under the null hypothesis and the alternative hypothesis. An estimated Bayes factor (null/alternative) suggested that the data were 143.62 times more likely to occur under the model including an effect of numerosity adaptation on numerosity discrimination, rather than the model without it.

In duration adaptation (Figure 3d), the mean PSE values in the duration discrimination task were significantly higher after adaptation to a short duration (67 msec; *M* = 257.67 msec, *SD* = 76.84 msec) compared to a long duration (600 msec; *M* = 214.84 msec, *SD* = 64.08 msec), *t*(19) = 3.50, *p* < .01, Cohen's *d* = .80. An estimated Bayes factor suggested that these data were 16.88 times more likely to occur under the model including an effect of duration adaptation on duration discrimination, rather than the model without it.

As shown in Figure 4b, the mean PSE values in duration discrimination task were marginally higher after adaptation to a low numerosity (*M* = 224.62 msec, *SD* = 52.64 msec) compared to a high numerosity (*M* = 211.89 msec, *SD* = 49.13 msec), but this difference failed to reach statistical significance, *t*(19) = 1.91, *p* > .05 = .071, Cohen's *d* = .43. An estimated Bayes factor suggested that these data were only 1.06 times more likely to occur under a model including an effect of numerosity adaptation on duration discrimination rather than a model without it.

As shown in Figure 4d, the mean PSE values in numerosity discrimination task were significantly higher after adaptation to a short duration (*M* = 36.59 dots, *SD* = 1.67 dots) compared to a long duration (*M* = 35.29 dots, *SD* = 1.72 dots), *t* (19) = 2.84, *p* < .05 = .013, Cohen's *d* = .64. An estimated Bayes factor suggested that these data were 5.24 times more likely to occur under the model including an effect of duration adaptation on numerosity discrimination, rather than the model without it.

In order to examine whether adaptation yielded changes not only in task accuracy as measured by the PSE values, but also precision, we analyzed the slope values obtained in each experimental condition. The assumption of normality was violated in the slope values. Thus, a series of Wilcoxon signed-rank tests were conducted to examine whether the slopes of the psychometric curves of the numerosity and duration discrimination tasks were significantly different after adapting to a low and high numerosity, and a short and long duration. No comparison reached statistical significance after using FDR-corrected significance thresholds.

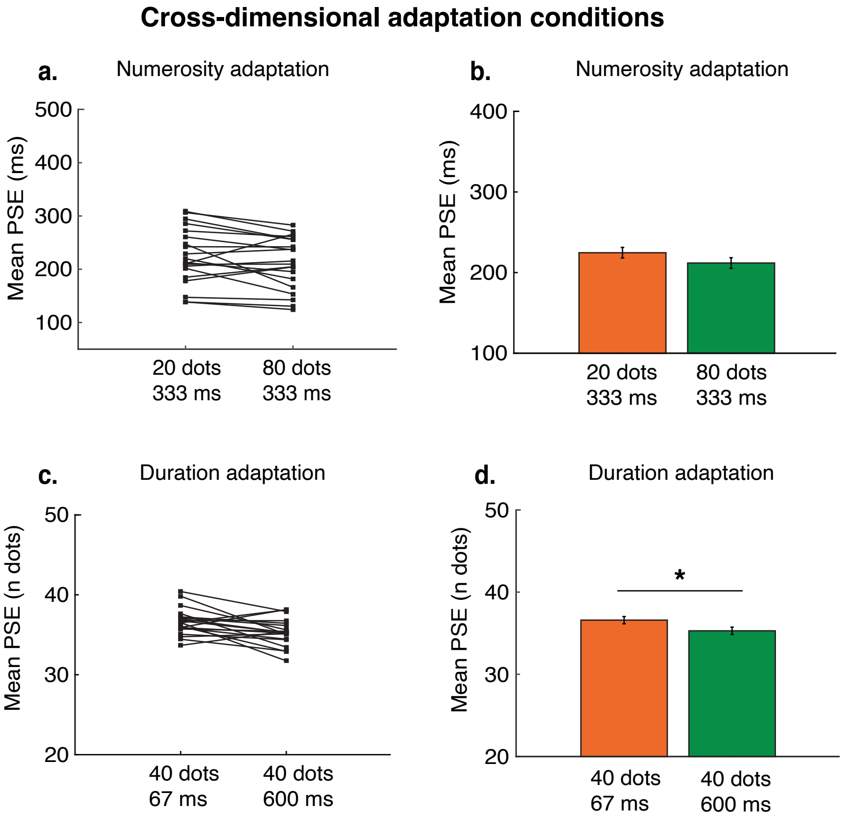

Figure 4. *PSE values in the cross-dimensional adaptation conditions per participant (left) and on a group level (right).* (b) On a group level, duration discrimination was not significantly affected by numerosity adaptation, (d) while numerosity discrimination was significantly affected by duration adaptation. Error bars represent 95% Confidence Intervals, adjusted for a within-subjects design (Loftus & Masson, 1994).

4. Discussion

The purpose of this study was to investigate whether numerosity and duration processing rely on a single magnitude system as postulated by the ATOM theory. To achieve this, we used cross-dimensional visual adaptation to numerosity and duration and a rapid adaptation paradigm. Our rationale was based on the idea that the aftereffects produced by visual adaptation are selective to the adapting stimulus, revealing dedicated coding strategies for that stimulus (see review by Webster, 2012). Hence, we hypothesized that if numerosity and time are processed by similar neural networks, then the visual aftereffects following numerosity and duration adaptation should affect duration and numerosity discrimination respectively. Our results partially confirm this hypothesis, since we found an unbalanced interaction between numerosity and duration perception.

More specifically, and in the unidimensional conditions, we found that visual adaptation to a low numerosity (20 dots) compared to a high numerosity (80 dots) altered the estimation of the reference numerosity (40 dots) by an average of 5 dots, in agreement with previous studies (Aagten-Murphy & Burr, 2016; Burr & Ross, 2008). Similarly, adapting to a short visual duration (67 msec) compared to a long duration (600 msec) altered the estimation of the reference duration (333 msec) by an average of 43 msec, confirming the work by Heron, Aaen-Stockdale, et al. (2012).

In the cross-dimensional adaptation conditions, our study shows that visual adaption to a short compared to a long duration altered numerosity discrimination judgments by an average of 1 dot. On the other hand, adapting to a low compared to a high numerosity did not significantly alter duration discrimination. Moreover, and based on the sequential analyses of the Bayes factors obtained (Schönbrodt et al., 2017; see Supplementary materials), there was not sufficient evidence to either support or reject the effect of numerosity adaptation on duration judgments. Since there was no definitive trend found, and to address a potential concern, increasing our sample size would not necessarily change this inconclusive finding.

A general theory on how adaptation operates on a neural level is that the adapting stimuli will cause the excitation of a large assembly (or network) of neurons which have the same type of specificity (Barlow & Foldiak, 1989). Based on this, the repeated presentation of a visual numerosity or duration could lead to the joint excitation of many neurons which are all tuned to numerosity and duration discrimination, thus leading to a common pattern of perceptual aftereffects (i.e., under- or overestimation). In other words, if adaptation to duration alters sensitivity to numerosity, then it can be inferred that both dimensions are detected by a common network (Webster, 2012).

The effects of adaptation can also be understood in terms of a Bayesian estimation framework. More specifically, Stocker and Simoncelli (2006) proposed that adaptation increases the signal-to-noise ratio resulting in changes in the likelihood function. Therefore, a Bayesian estimator model can account for the perceptual aftereffects and changes in the discrimination threshold induced by adaptation (Stocker & Simoncelli, 2006). In respect to our findings, the unidirectional influence of time on numerosity perception is corroborated by the work of Lambrechts et al. (2013) and Martin et al. (2017) who used a Bayesian approach. According to these studies, a plausible explanation for the unidirectional influence of time on numerosity perception would be the conceptualization of the ATOM theory in terms of a Bayesian framework and by inferring the existence of multiple priors (Martin et al., 2017). Martin et al. (2017) suggested that when sensory information needed for numerosity processing accumulate over a varying duration (short or long), then the varying degrees of uncertainty associated with temporal processing can add noise to the sensory accumulation of numerosity information, altering thus, the perception of numerosities (p.11-12).

Hence, we argue that although unbalanced, there is indeed an interaction of numerosity and time processing in the brain in accordance with the ATOM theory (Bueti & Walsh, 2009; Dormal, Dormal, et al., 2012; Hayashi, Kanai, et al., 2013; Hayashi, Valli, et al., 2013; Skagerlund et al., 2016; Walsh, 2003). This is further exemplified by the same pattern of overestimating and underestimating the reference numerosity or duration after exposure to a low and high magnitude respectively (see Figure 2 and Figure 3). Hence, we argue that there are dedicated neural mechanisms for processing both numerosity and duration, with both numerosity and time perception undergoing adaptation-based recalibration (Anobile et al., 2016; Heron et al., 2013).

In order to further explain the unbalanced interaction we found between numerosity and duration processing, a possible explanation could reside on the size of the receptive fields (RFs) of neurons tuned to numerosity and duration processing. More specifically, there is robust evidence showing that numerosity adaptation is spatially selective (Aagten-Murphy & Burr, 2016; Burr & Ross, 2008) which could be attributed to the relatively circumscribed RFs of neurons tuned to numerosity (Anobile et al., 2016). On the other hand, the spatial selectivity of the duration after-effects remains unclear (Heron, Roach, et al., 2012; Li et al., 2015; Maarseveen et al., 2017), which might imply that the size of the RFs of neurons tuned to duration is larger and much less defined compared to the RFs of neurons tuned to numerosity. Hence, it is reasonable to assume that if duration and numerosity rely on similar cortical networks, then the larger RFs of neurons tuned to duration are more likely to affect the response of the smaller RFs of neurons tuned to numerosity. To further examine this possibility, we increased the size of the dot stimuli used as numerosity adapters and retested 12 participants from our original sample on duration discrimination (see Supplementary materials). We found no significant effect of numerosity adaptation on duration discrimination, which could imply that the RFs of neurons tuned to duration processing are less sensitive to changes in numerosity and object size. Nevertheless, it should be mentioned that the method of adaptation cannot separate the aftereffects induced on individual neurons from aftereffects induced on a neural network level, rendering the aforementioned account on the size of the RFs of neurons only speculative.

Perceptual adaptation is thought to induce changes in sensitivity which appear early in the visual system and can spread to later stages, with complex aftereffects such as the ones examined in our study reflecting changes inherited from earlier levels (Webster, 2012). Based on this, another explanation for the unbalanced interaction we found in the cross-dimensional adaptation conditions could be that numerosity and duration adaptation occurs at different processing stages leading to a differential influence of one over the other. More specifically, a recent functional magnetic resonance imaging (fMRI) study found that activation in the IPS but not V1, classified numerosity well, both before and after adaptation to a high (80 dots) numerosity (Castaldi et al., 2016). Similarly, there is robust evidence for the existence of numerosity selective neurons in the parietal cortex in humans (Harvey et al., 2013; Harvey & Dumoulin, 2017a; Piazza et al., 2004) and non-human primates (Nieder, 2012; Nieder & Miller, 2004a). On the other hand, duration adaptation could involve lower areas of the visual cortex, with Heron et al. (2013) finding that duration adaptation precedes multisensory integration. The authors argued that there are duration selective networks in early areas of the visual and auditory system. Several neurophysiological studies have suggested that neurons in early visual and auditory systems of non-human animals are selective for temporal-frequency or tuned to duration (Brand et al., 2000; Duysens et al., 1996; Eriksson et al., 2008; Ghose & Maunsell, 2002; Hawken et al., 1996; Mendelson & Cynader, 1985; Pérez-González et al., 2006).

Hence, if duration adaptation involves lower areas of the visual cortex compared to the more parietal areas involved in numerosity adaptation, this could indicate that there is a processing hierarchy where temporal information processing precedes numerical processing. Based on this speculated processing hierarchy, time could encompass numerosity at a low perceptual level, and the information derived from both dimensions could be then integrated in the parietal cortex to generate guided action, as ATOM postulates. Nevertheless, the proposed processing hierarchy is rather unlikely since recent studies do implicate the lower areas of the visual cortex in numerosity processing (Fornaciai et al., 2017; Park et al., 2016). Therefore, and in order to elucidate how the adaptation aftereffects are produced within and across dimensions (i.e., numerosity and duration), future research could help identifying how neurons adapt at each stage and how adaptation-induced plasticity in early processing stages propagates throughout the processing hierarchy (Clifford et al., 2007).

Long and Beaton (1981) were one of the first to demonstrate an effect of numerosity on duration perception. More recent studies have also reported a strong interference of numerosity on duration processing (Alards-Tomalin et al., 2016; Dormal et al., 2006; Hayashi, Valli, et al., 2013), a finding which is not in agreement with the weak effect of numerosity adaptation on duration discrimination we found in our study. However, all the aforementioned studies used very low numerosities (up to 10 dots) which could account for the observed discrepancy by inferring distinct mechanisms for processing low compared to high numerosities. For instance, perceiving low numerosities appears to be less affected by low-level stimulus characteristics, whereas perceiving high numerosities relies more heavily on density and size information (Dakin et al., 2011; Gebuis & Reynvoet, 2012; Zimmermann & Fink, 2016). Moreover, numerosities within the subitizing range (up to 4 items) appear to rely more heavily on attentional resources compared to numerosities in the estimation range, a finding which further supports the existence of distinct processing mechanisms (Anobile et al., 2012; Burr et al., 2011; Burr et al., 2010). Further research manipulating the range of numerosities and durations used could provide a greater insight on whether there are distinct mechanisms for processing low compared to high numerosities, and sub-compared to supra-second durations.

It is also worth mentioning that we did not find any statistically significant differences in the average PSE and slope values when the adaptation stimuli were presented to the left versus right side in each adaptation condition-task. This could be an outcome of successful counterbalancing of the presentation side (left vs right) and the order of the presentation side (adaptation trials starting from the left or right side). Nevertheless, the aforementioned lack of differences could be considered as being at odds with the 'mental number line' and the spatial-numerical association of response codes (SNARC) effect. These concepts describe an introspective left-to-right arrangement of ascending numbers. Based on this, shorter reaction times are recorded when low numbers are presented to the left, and high numbers are presented to the right (Cohen Kadosh et al., 2008; Dehaene et al., 1993). However, no study to our knowledge has found evidence for the SNARC effect when using high numerosities (> 30 dots), which could also account for the lack of differences in our study given the range of numerosities we used.

In the case of numerosity adaptation, some studies suggest that the adaptation effects examined are in response to density and not numerosity mechanisms (Durgin, 2008; Sun et al., 2017; Tibber et al., 2012). Our rationale for choosing the specific numerosities used as adapters (20 vs 80 dots) and the rest of our stimulus characteristics (i.e., dot size, eccentricity), was based on the methodology used by a number of similar studies (Burr & Ross, 2008; Castaldi et al., 2016; Fornaciai et al., 2016; Turi et al., 2015), and the model proposed by Anobile et al. (2016) which describes the eccentricity and density parameters implicated in inferring adaptation to numerosity and not texture. Thus, we are fairly confident that our experimental design was indeed appropriate for examining visual adaptation to numerosity and not texture-like mechanisms.

Another potential concern is that the rapid adaptation paradigm we used (100 trials with no top-up adaptation trials) may have hindered the full potential of numerosity and duration adaptation on duration and numerosity discrimination respectively. We do not believe this is the case because in the unidimensional adaptation conditions, this rapid adaptation paradigm was effective in inducing robust perceptual distortions in the expected direction. Therefore, it seems unlikely that this adaptation protocol could pose a serious methodological limitation in the cross-dimensional conditions.

5. Conclusions

Our study shows that both numerosity and time perception adapt under brief exposures and have a moderate ability to cross-adapt. We found a unidirectional influence of duration adaptation on numerosity judgments, with numerosity adaptation not affecting duration judgments significantly. We argue that numerosity and time processing rely on partially overlapping neural networks.

Chapter 4

Distinct temporal mechanisms modulate numerosity perception

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Abstract

Our ability to process numerical and temporal information is an evolutionary skill thought to originate from a common magnitude system. In line with a common magnitude system, we have previously shown that adaptation to duration alters numerosity perception. Here, we investigate two hypotheses on how duration influences numerosity perception. A channel-based hypothesis predicts that numerosity perception is influenced by adaptation of onset/offset duration channels which also encode numerosity or wire together with numerosity channels (duration/numerosity channels). Hence, the onset/offset duration of the adapter is driving the effect regardless of the total duration of adaptation. A strength-of-adaptation hypothesis predicts that the effect of duration on numerosity perception is driven by the adaptation of numerosity channels only, with the total duration of adaptation driving the effect regardless of the onset/offset duration of the adapter. We performed two experiments where we manipulated the onset/offset duration of the adapter, the adapter's total presentation time, and the total duration of the adaptation trial. The first experiment tested the effect of adaptation to duration on numerosity discrimination, whereas the second experiment tested the effect of adaptation to numerosity and duration on numerosity discrimination. We found that the effect of adaptation to duration on numerosity perception is primarily driven by adapting duration/numerosity channels, supporting the channel-based hypothesis. In contrast, the effect of adaptation to numerosity on numerosity perception appears to be driven by the total duration of the adaptation trial, supporting the strength-of-adaptation hypothesis. Thus, we show that adaptation of at least two temporal mechanisms influences numerosity perception.

1. Introduction

Imagine yourself being at a rather boring party and feeling quite hungry. Suddenly a few plates with appetizers appear, and you have to act fast, since more and more people approach them and the amount of food decreases rapidly. Within a few seconds, you are able to detect the plate with the most food on it, the smallest number of people around it, and the fastest access to it. Soon you manage to satiate your hunger, feeling proud of your efficient action.

This is only one example of the many situations illustrating how humans, among many other species, are able to process and integrate information about quantity and time in order to act efficiently in their environment (Dehaene et al., 1998; Grondin, 2010; Leon & Shadlen, 2003).

This is the core idea behind "a theory of magnitude" (ATOM), which proposes that numerosity (i.e., the number of items in a set), time, and space are magnitudes derived from a partly shared magnitude system and linked by a common metric (Bueti & Walsh, 2009; Walsh, 2003; see also Cantlon et al., 2009; Cappelletti et al., 2011). According to ATOM, the interaction of these magnitudes is essential for learning about our environment and generating action.

How do these different magnitudes interact? From a theoretical perspective, Meck and Church (1983) proposed the "mode control" model, uniting number and time processing (Gibbon et al., 1984; Meck et al., 1985). This model proposes that number and time are represented by an internal clock that consists of "pacemaker"-type pulses which accumulate in a counter. Based on this model, number and duration discrimination rely on a single magnitude system which operates in either the counting or the timing mode (Fetterman, 1993). From an experimental perspective, a number of behavioral (Alards-Tomalin et al., 2016; Cappelletti et al., 2009; Cappelletti, Freeman, & Butterworth, 2011; Chun et al., 2018; Dormal et al., 2006; Gilaie-Dotan et al., 2014; Javadi & Aichelburg, 2012; Lambrechts et al., 2013; Martin et al., 2017; Tokita & Ishiguchi, 2011; Tsouli, Dumoulin, et al., 2019) and neuroimaging (Bueti & Walsh, 2009; Cappelletti et al., 2014; Castelli et al., 2006; Hayashi, Kanai, et al., 2013; Javadi et al., 2014) studies provide support for a partly shared processing system for numerosity and time, whereas other studies suggest that numerosity and time are independent and are processed by distinct mechanisms (Agrillo et al., 2010, 2013).

One useful behavioral method for inferring about the neural underpinnings of a given perceptual property is sensory adaptation (Frisby, 1979). Specifically, after prolonged exposure to a specific stimulus, both the response of the neurons processing that stimulus and the perceptual experience of a subsequently presented (similar) stimulus change (Grill-Spector et al., 2006; Kohn, 2007; Mollon, 1974; Thompson & Burr, 2009; Wade & Verstraten, 2005). A number of models have been proposed to account for the neural mechanisms underlying adaptation, including neuronal fatigue with less overall activation (fatigue model), fewer neurons responding (sharpening model), and less processing time (facilitation model; see review by Grill-Spector et al., 2006).

Numerosity, similarly to other visual properties such as color or contrast, is susceptible to adaptation (Anobile et al., 2016; Burr et al., 2017; Burr & Ross, 2008). Even brief adaptation to a visual numerosity changes the perception of a subsequently viewed numerosity at the same location (Aagten-Murphy & Burr, 2016; Castaldi et al., 2016). Likewise, time is also susceptible to adaptation, with adaptation to a previous duration influencing the perception of a subsequently presented duration (Becker & Rasmussen, 2007; Heron, Aaen-Stockdale, et al., 2012; Heron et al., 2013; Johnston et al., 2006; Li et al., 2017; Maarseveen et al., 2017; Magnussen & Johnsen, 1986; Shima et al., 2016).

We have recently replicated the finding that both numerosity and duration adapt, using very few trials and brief exposures (Aagten-Murphy & Burr, 2016; Tsouli, Dumoulin, et al., 2019). In addition, we explored the interaction between numerosity and time perception using a cross-adaptation paradigm. We hypothesized that if numerosity and time rely on a shared processing network, then adaptation to numerosity should affect temporal judgments and adaptation to duration should affect numerosity judgments. We found a unidirectional effect of adaptation to duration on numerosity discrimination, where adaptation to visual duration altered the perception of numerosity. However, adaptation to numerosity did not affect the perception of duration. Hence, we concluded that numerosity and time processing rely on partially overlapping neural networks.

Based on these findings, the first goal of the present study was to elucidate how duration affects numerosity perception. Specifically, we investigated two hypotheses, even though these hypotheses are not mutually exclusive. First, there is evidence supporting the existence of numerosity-selective “channels” or groups of neurons tuned to a preferred numerosity (Harvey et al., 2013, 2015; Harvey & Dumoulin, 2017a; Kutter et al., 2018; Piazza et al., 2004). Likewise, there is evidence suggesting that there are duration-selective channels tuned to a preferred duration that are dedicated to processing specific temporal features (Hayashi et al., 2015; Heron, Aaen-Stockdale, et al., 2012; Heron et al., 2019; Ivry, 1996; Motala et al., 2018; Protopapa et al., 2019; Walker et al., 1981). The duration channels revealed using adaptation appear to encode the interval between the onset and offset duration of an event (Heron, Aaen-Stockdale, et al., 2012; Maarseveen et al., 2019), a finding which is further supported by neurophysiological studies in animals (Duysens et al., 1996; Ehrlich et al., 1997; He et al., 1997).

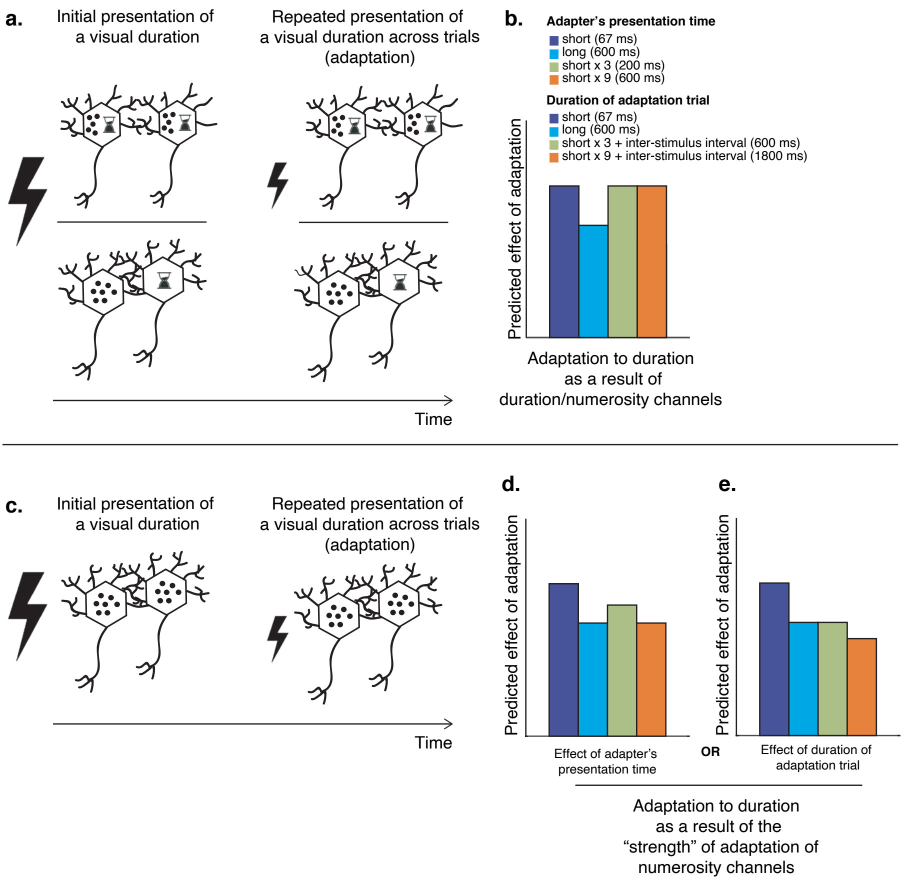

Figure 1. *Hypothesized mechanisms of adaptation to duration on underlying neural responses and predicted outcomes.* The initial presentation of a duration would first elicit a high neuronal response, but upon repeated presentation of that duration across trials, that response would be decreased due to adaptation. (a) According to the duration/numerosity-channels hypothesis, adaptation alters the response of channels encoding both duration and numerosity (or neurons tuned to duration and neurons tuned to numerosity which wire together) which are tuned to the onset/offset interval of a duration event. (b) Hence, the adaptation conditions where the adapter's onset/offset duration (i.e., 67 ms) is the same (dark-blue, green, and orange bars) will yield similar adaptation effects, regardless of other duration parameters (e.g., the duration of the adapter's total presentation time or the total duration of the adaptation trial). (c) According to the strength-of-adaptation hypothesis, adaptation alters the response of numerosity channels only, with the longest duration (600 or 1,800 ms) driving the adaptation effect. (d) Thus, the adaptation conditions with the longest total adapter presentation time (light-blue and orange bars) or (e) the longest total duration of the adaptation trial (orange bars) will lead to stronger adaptation, even if these durations are composed of a short onset/offset duration (green and orange bars).

Based on the foregoing, we hypothesized that the effect of duration on numerosity (Tsouli, Dumoulin, et al., 2019) could reflect the adaptation of onset/offset duration channels which influence numerosity perception. This could occur either because these duration channels are also tuned to numerosity or because channels tuned to either duration or numerosity wire together (duration/numerosity channels; Figure 1a). Both possibilities would be in accordance with the idea of a common processing network for numerosity and time (Bueti & Walsh, 2009; Cantlon et al., 2009; Cappelletti, Freeman, & Cipolotti, 2011; Gibbon et al., 1984; Meck et al., 1985; Meck & Church, 1983; Walsh, 2003).

The second hypothesis suggests that the effect of adaptation to duration is driven by the total strength of adaptation of numerosity-selective channels only. Specifically, a common notion in adaptation research suggests that a longer adaptation period results in stronger perceptual aftereffects (Kohn, 2007). This would mean that a long duration leads to stronger adaptation not as a result of adapting duration/numerosity channels but as a result of adapting numerosity channels for a long period. Since the strength-of-adaptation hypothesis would entail the adaptation of numerosity channels only, it is not conceptually related to the idea of a shared magnitude system as the ATOM postulates (Bueti & Walsh, 2009; Walsh, 2003).

Based on these hypotheses, we made the following predictions. If the effect of adapting to duration is caused by adaptation of duration/numerosity channels, the channels with preferred durations closest to that of the adapter would be most strongly adapted, and those with different duration preferences would be less strongly adapted. More specifically, the initial presentation of a duration with a short onset/offset (e.g., 67 ms) would elicit a high response from duration/numerosity channels tuned to a short duration. After repeated presentation of that short duration across adaptation trials, these channels would adapt and show a decreased response (Figure 1a). This would alter the perceived numerosity of a subsequently presented stimulus, similar to how adaption to a low numerosity would alter numerosity perception (i.e., overestimation of the subsequently presented numerosity; Burr & Ross, 2008). However, given the duration preference of these channels, a single presentation of a short onset/offset duration would produce the same adaptation effects as would a repeated presentation (three or nine times) of the same duration within the same adaptation trial (Figure 1b, dark-blue, green, and orange bars). Therefore, although a repeated presentation would lead to a longer total duration of the adapter stimulus, the adaptation effects would still be similar, due to the assumed existence of duration/numerosity channels tuned to a short onset/offset duration. In the case of adapting to duration/numerosity channels tuned to a long onset/offset duration (e.g., 600 ms; Figure 1b, light-blue bar), the predicted effect on numerosity perception would be similar to that produced by adaptation to a high numerosity (i.e., underestimation of the subsequently presented numerosity).

According to the strength-of-adaptation hypothesis, the initial presentation of a short duration stimulus would produce a high neural response on numerosity channels only (Figure 1c). After repeated presentation of that short duration across adaptation trials, the numerosity channels would adapt and show a decreased response. However, contrary to the duration/numerosity-channels hypothesis, the repeated presentation of that duration (three or nine times) within the same adaptation trial would lead to further adaptation of the numerosity channels due to the longer total duration produced. This would alter the perception of a subsequently presented numerosity stimulus. Thus, the strongest adaptation effect would be produced by the longest duration, regardless of the specific temporal elements this duration has (i.e., onset/offset duration; Figure 1d and 1e).

In summary, the first hypothesis entails the involvement of duration/numerosity channels, where the effect of adaptation is driven by the onset/offset duration of the adapter, whereas the second hypothesis entails the involvement of numerosity channels only, where the effect of adaptation is driven by the total duration of the adapter, even if the onset/offset duration of the adapter is short.

Based on our research goals we conducted two experiments; the first examined the effect of adaptation to duration on numerosity discrimination, and the second examined the combined effect of adaptation to numerosity and duration on numerosity discrimination. In both experiments, we manipulated the adapter's onset/offset duration, its presentation time, and the total duration of the adaptation trial. In order to test the duration/numerosity-channels hypothesis, the preferred duration was operationally defined as the onset/offset duration of the adapter (Heron, Aaen-Stockdale, et al., 2012; Maarseveen et al., 2019). We hypothesized that the duration conditions comprising a short (67 ms) versus a long (600 ms) onset/offset duration should yield relative over- and underestimation of the reference numerosity, respectively, similar to the effect produced by adapting to a low versus a high numerosity. Conversely, in order to test the hypothesis on the strength of adaptation of numerosity channels, the adapter's total presentation time or the total duration of the adaptation trial was hypothesized to produce the strongest adaptation effects, regardless of the onset/offset duration of the adapter.

We found that the effect of adaptation to duration on numerosity discrimination in our first experiment was mainly driven by adapting duration/numerosity channels. In contrast, the effect of adaptation to numerosity and duration on numerosity discrimination in our second experiment appeared driven by the total duration of the adaptation trial. Thus, we found that different temporal mechanisms modulate numerosity perception.

2. Methods

2.1. Participants

Thirty participants (20 women, M_{age} = 23.35 years, SD_{age} = 2.62; 10 men, M_{age} = 23.40 years, SD_{age} = 3.86) participated in Experiment 1. Twenty-four participants (18 women, M_{age} = 22.23 years, SD_{age} = 2.46; six men, M_{age} = 24.0 years, SD_{age} = 2.37) participated in Experiment 2. All participants had normal or corrected-to-normal visual acuity and were unaware of the purpose of the study. Participants gave written informed consent and received a monetary reward or course credits. The experiments were conducted in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the Faculty of Social and Behavioural Sciences of Utrecht University.

2.2. Apparatus and stimuli

The apparatus and stimuli were identical to the ones described in our previous study (Tsouli, Dumoulin, et al., 2019). Briefly, participants sat at a distance of about 60 cm from a 60 × 34 cm Asus LCD monitor with a resolution of 2,560 × 1,440 and a refresh rate of 60 Hz. The display was linearized using a photometer (Mavo Monitor USB, Gossen, Nürnberg, Germany). The stimuli (viewed binocularly) were circular patches containing an equal proportion of black and white dots displayed on a mean-luminance background (60 cd/m2) at 80% Michelson contrast. Each dot had a diameter of 0.2° of visual angle, and the circular patches had a diameter of 12°. In each trial, dots were scattered randomly within the circular patches and were not allowed to overlap. The center of the dot patches was at 8° eccentricity left of fixation for the first half of the trials and right of fixation for the other half (100 trials in total), with the side block counterbalanced across participants. All stimuli were generated and presented using MATLAB (Version 2016b; MathWorks, Inc., Natick, MA) and the Psychophysics Toolbox (Version 3.0.13; Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

2.3. Procedure

Both Experiment 1 (adaptation to duration) and Experiment 2 (adaptation to numerosity and duration) had four duration adaptation conditions (Figure 2). In Conditions 1 (67 ms) and 2 (600 ms), the adapter's onset/offset duration was equal to the adapter's total presentation time and the total duration of the adaptation trial. In Condition 3, the adapter's onset/offset duration was 67 ms, its total presentation time was 200 ms (three repetitions of 67 ms interleaved with a 133-ms interstimulus interval [ISI]), and the total duration of the adaptation trial was 600 ms. In Condition 4, the adapter's onset/offset duration was 67 ms, its total presentation time was 600 ms (nine repetitions of 67 ms interleaved with a 133-ms ISI), and the total duration of the adaptation trial was 1,800 ms.

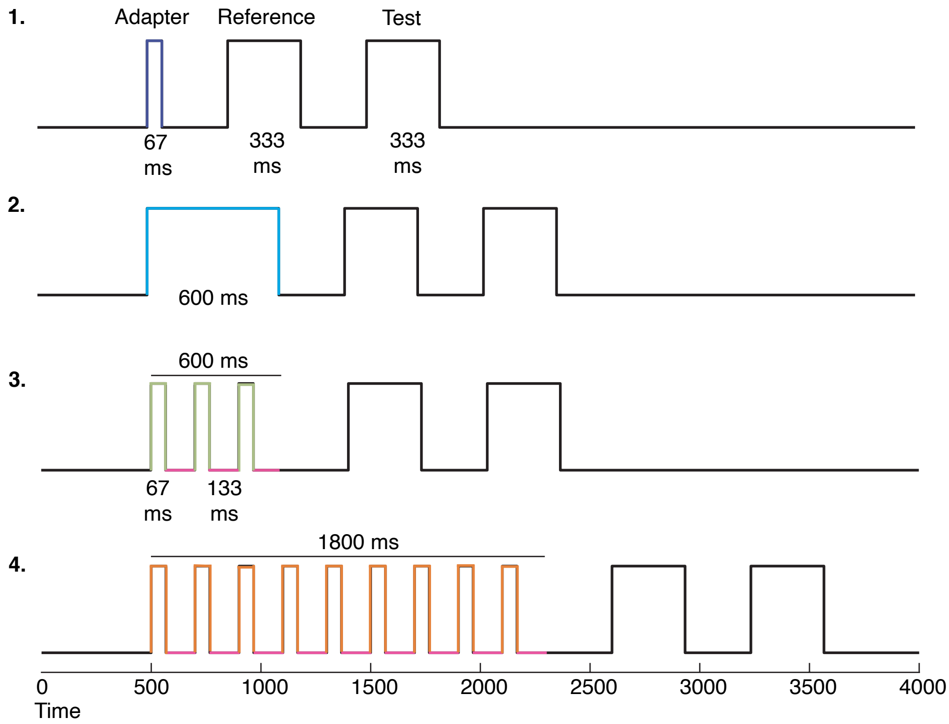

Figure 2. *Schematic representation of the adaptation to duration conditions in Experiments 1 and 2.* In Conditions 1 (67 ms) and 2 (600 ms), the adapter's onset/offset duration was equal to its total presentation time and the total duration of the adaptation trial. In Condition 3, the adapter's onset/offset duration was 67 ms, its total presentation time was 200 ms (three repetitions of 67 ms), and the total duration of the adaptation trial was 600 ms. In Condition 4, the adapter's onset/offset duration was 67 ms, its total presentation time was 600 ms (nine repetitions of 67 ms), and the total duration of the adaptation trial was 1,800 ms. This stimulus design evaluated the influence of the adapter's onset/offset duration (67 vs. 600 ms) compared to the total duration of the adaptation trial (67 vs. 600 vs. 1,800 ms).

In each trial, the adapter was shown first and lasted for one of the four duration adaptation conditions. After a 300-ms pause, the reference patch was presented for 333 ms at the same location as the adapter, followed by another 300-ms pause, and then the test patch appeared for 333 ms at the opposite side of fixation. Our choice of presenting the adapter and reference stimulus on one side and the test stimulus on the opposite side was based on findings suggesting that adaptation to numerosity is spatially specific (Aagten-Murphy & Burr, 2016; Arrighi et al., 2014; Burr & Ross, 2008).

In the beginning of each experiment, participants were given the following instructions:

> *You will see one cloud of dots appearing on one side of the screen, followed by another cloud of dots in the same location, and then another cloud of dots in the opposite location. Your task is to respond as fast and accurately as possible (guessing if unsure) which of the two clouds you saw last seemed to have more dots. On the keyboard placed in front of you, press the "f" key if you think it was the left cloud of dots that had more dots, or the "j" key if you think it was the right cloud that had more dots.*

The paradigm used was a two-alternative forced-choice task. After the participant gave a response, the next trial started after 500 ms.

Experiment 1: Adaptation to duration

The visual stimuli used as duration adapters comprised 20, 40, or 80 dots, and the respective reference patches also comprised 20, 40, or 80 dots (Figure 3a). The numerosity of the test patch varied from trial to trial using the minimum-expected-entropy staircase method (Saunders & Backus, 2006). Since the adapter and reference stimuli were matched in numerosity but not duration, no adaptation to numerosity was expected to occur, only adaptation to duration (Figure 3b). Regarding our choice of numerosity stimuli, the effect of adaptation to duration on numerosity discrimination that we found in our previous study (Tsouli, Dumoulin, et al., 2019) was induced using numerosity and reference stimuli of 40 dots. However, it could be possible that the observed adaptation phenomenon is affected by the specific visual stimulus used as a duration adapter. Therefore, we now investigated whether the effect of adaptation to duration on numerosity perception would be present with an intermediate numerosity of 40 dots as we did before, and also with a low (20 dots) and a high (80 dots) numerosity. The order of the duration conditions and the numerosity stimuli used as visual duration adapters was counterbalanced across participants.

Experiment 2: Adaptation to numerosity and duration

The visual stimuli used as numerosity adapters comprised 20, 40, or 80 dots, and the reference patch always comprised 40 dots (Figure 3c). Similar to Experiment 1, the numerosity of the test patch varied from trial to trial using the minimum-expected-entropy staircase method (Saunders & Backus, 2006). Since the adapter and reference stimuli were not matched in numerosity or duration, we expected adaptation to numerosity and duration to occur. The numerosity adapters were displayed for one of the four duration conditions described earlier. Participants adapted to a low (20 dots) or high (80 dots) numerosity, which was expected to result in over- or underestimation of the reference numerosity, respectively (Aagten-Murphy & Burr, 2016; Tsouli, Dumoulin, et al., 2019). The condition where both the adapter and the reference numerosity were 40 dots was identical to Experiment 1 and served as a control condition used for replicating the findings of Experiment 1. Participants were given the same instructions as in Experiment 1, and the paradigm used was again a two-alternative forced-choice task. The order of the duration conditions and the numerosity stimuli used as numerosity and duration adapters was counterbalanced across participants.

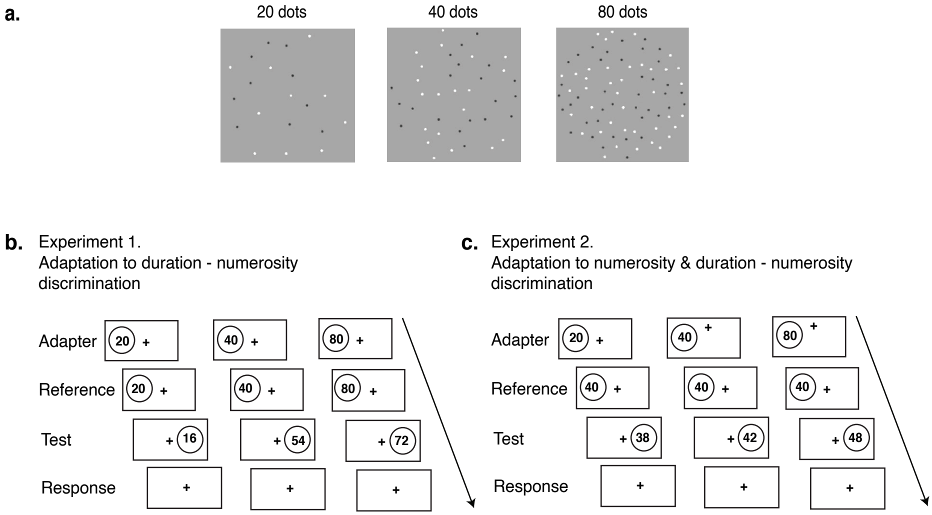

Figure 3. *(a) The stimuli used as duration and numerosity adapters and a schematic representation of a single trial in (b) Experiments 1 and (c) 2.* In Experiment 1, the stimuli used as duration adapters and reference stimuli comprised 20, 40, or 80 dots. Given that the adapter and reference stimuli were matched only in numerosity, not duration, no adaptation to numerosity was expected to take place, only adaptation to duration. The numerosity of the test stimuli varied based on a staircase method. In Experiment 2, the stimuli used as numerosity and duration adapters comprised 20, 40, or 80 dots and the reference stimulus was always 40 dots. Given that the adapter and reference stimuli were not matched in numerosity or duration, adaptation to numerosity and duration was expected to take place. Similar to Experiment 1, the numerosity of the test stimuli varied based on a staircase method. In Experiment 2, the condition where the adapter and reference stimuli had 40 dots was identical to Experiment 1 and was used for replicating the respective condition in Experiment 1. In both experiments, participants were instructed to respond, as fast and accurately as possible, which of the two clouds presented last appeared to contain more dots, by pressing (on a keyboard) the F key for the left cloud or the J key for the right cloud.

3. Data Analysis

All data analyses were conducted using MATLAB, SPSS (Version 24.0; SPSS Inc., Chicago, IL), and JASP (Version 0.8.1.2; JASP Team, 2019).

After each experiment, we first collapsed the data across presentation side blocks (left vs. right). This yielded 100 data points per condition. We subsequently sorted these data points on the numerosity of the test stimulus. For these sorted data, we then created 10 equally sized bins (i.e., containing the data of 10 trials each). We then fitted these data with cumulative Gaussian functions to yield estimates of the point of subjective equality (PSE) and slope for each condition, and used the PSE and slope values for subsequent analyses (Tsouli, Dumoulin, et al., 2019).

In addition, we transformed the PSE values into values corresponding to the just-noticeable difference (JND) and performed the same statistical analyses. In order to obtain the JND values for each participant, we first calculated a standardized slope for each numerosity condition using the following formula:

$$standardized\ slope = \sqrt{\frac{\Sigma(slope^2)}{n\ (= 4\ duration\ conditions)}} \tag{1}$$

Our choice of calculating a standardized slope for each participant using Equation 1 was supported by the fact that there were no statistically significant differences in the slope values obtained from the four duration conditions within each numerosity condition, as assessed by a series of Wilcoxon signed-rank tests (due to violation of the normality assumption; false discovery rate [FDR]–corrected significance thresholds) in either Experiment 1 or 2 (see also Results).

The JND values in Experiment 1 were then calculated using the formula:

$$\mathrm{JND}\text{: } (PSE - reference\ numerosity)/standardized\ slope, \tag{2}$$

where the reference numerosity was 20, 40, or 80 dots, corresponding to the respective numerosity condition, and the standardized slope was that of the respective numerosity condition for each participant). The same formulas were used in Experiment 2, with the only difference being the reference numerosity used in Equation 2, which was always 40 dots.

Given that adaptation stimuli were presented at one side (e.g., left) for half of the trials and at the opposite side (e.g., right) for the other half, we wanted to examine whether this design would yield significant differences in our measurements. We calculated the average JND, PSE, and slope values for the left versus right presentation side across duration conditions for each numerosity-stimulus condition. We then performed nonparametric statistical tests, since a number of the measurements obtained were not normally distributed as assessed by box plots and the Shapiro–Wilk test. In Experiment 1, the JND values obtained when the adapter and reference stimulus were presented on the left side were significantly lower compared to when the adapter and reference stimulus were presented on the right side, in every numerosity-stimulus condition (adapter and reference stimulus = 20 dots: $\mathrm{Mdn}_{\mathrm{left}} = -0.49$, $\mathrm{Mdn}_{\mathrm{right}} = -0.15$, $Z = -2.81$, $p = 0.008$; adapter and reference stimulus = 40 dots: $\mathrm{Mdn}_{\mathrm{left}} = -1.02$, $\mathrm{Mdn}_{\mathrm{right}} = -0.46$, $Z = -2.91$, $p = 0.008$; adapter and reference stimulus = 80 dots: $\mathrm{Mdn}_{\mathrm{left}} = -1.11$, $\mathrm{Mdn}_{\mathrm{right}} = -0.46$, $Z = -2.27$, $p = 0.02$; FDR-corrected significance thresholds). The same was true for the PSE values (adapter and reference stimulus = 20 dots: $\mathrm{Mdn}_{\mathrm{left}} = 17.71$ dots, $\mathrm{Mdn}_{\mathrm{right}} = 19.41$ dots, $Z = -2.97$, $p = 0.009$; adapter and reference stimulus = 40 dots: $\mathrm{Mdn}_{\mathrm{left}} = 33.56$ dots, $\mathrm{Mdn}_{\mathrm{right}} = 36.91$ dots, $Z = -2.23$, $p = 0.03$; adapter and reference stimulus = 80 dots: $\mathrm{Mdn}_{\mathrm{left}} = 66.08$ dots, $\mathrm{Mdn}_{\mathrm{right}} = 73.60$ dots, $Z = -2.46$, $p = 0.02$; FDR-corrected). Nevertheless, no significant differences were found in the slope values, and no significant differences were found in the JND, PSE, or slope values in Experiment 2 using FDR-corrected significance thresholds. Moreover, there was no statistically significant effect of the presentation side block (adaptation trials starting from the left or right side) on the JND, PSE, or slope values in either experiment. Therefore, we decided to collapse all data across blocks and presentation sides.

4. Results

Adaptation of duration/numerosity channels affects numerosity discrimination after adaptation to duration (Experiment 1)

First, we examined which JND, PSE, and slope values differed using frequentist analyses. The JND and PSE values obtained from the numerosity-discrimination task were normally distributed in almost all duration adaptation conditions. The two exceptions were the JND values obtained after adapting to duration Condition 1, using 80 dots as a visual duration adapter and reference stimulus, as assessed by box plot and the Shapiro–Wilk test ($p = 0.002$); and the PSE values obtained after adapting to duration Condition 1, also when using 80 dots as a visual duration adapter and reference stimulus ($p = 0.031$). The slope values obtained were not normally distributed in almost all conditions. Therefore, we used nonparametric statistical tests (Friedman for assessing main effects, and Wilcoxon signed-rank tests as post hoc tests) for all comparisons. We corrected the significance thresholds of post hoc tests using FDR correction where applicable (see also Supplementary materials for the individual participants' data).

As seen in Figure 4a and 4b, there were no statistically significant differences in the JND, PSE, or slope values after adaptation to duration using 20 dots as a visual duration adapter and reference stimulus—both JND and PSE: $\chi^2(3) = 4.52$, $p = 0.21$; slope: $\chi^2(3) = 0.92$, $p = 0.82$. There were statistically significant differences in the JND and PSE values using 40 dots—both JND and PSE: $\chi^2(3) = 15.52$, $p = 0.001$. No statistically significant differences were found in the slope values, $\chi^2(3) = 2.60$, $p = 0.46$. The same was true using 80 dots—both JND and PSE: $\chi^2(3) = 13.96$, $p = 0.003$ (see Tables 1 and 2 for post hoc comparisons). No statistically significant differences were found in the slope values, $\chi^2(3) = 2.32$, $p = 0.51$.

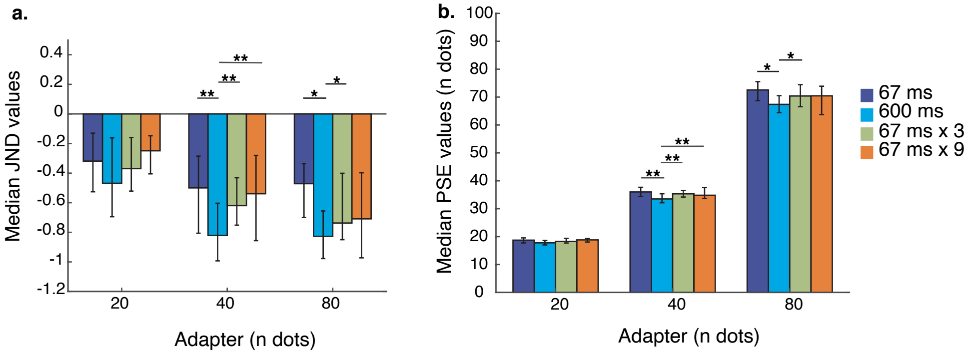

Figure 4. *(a) Median just-noticeable difference and (b) point of subjective equality for Experiment 1 (adaptation to duration).* The x-axis displays the numerosity of the visual duration adapters (20, 40, and 80 dots) and reference stimuli (20, 40, and 80 dots, respectively). The y-axis displays the median just noticeable difference or point of subjective equality obtained from the numerosity-discrimination task. The colored bars correspond to the four adaptation conditions (see also Figure 2). The dark-blue bars correspond to Condition 1 (adapter's onset/offset duration: 67 ms = total duration of the adaptation trial). The bright-blue bars correspond to Condition 2 (adapter's onset/offset duration: 600 ms = total duration of the adaptation trial). The green bars correspond to Condition 3 (adapter's onset/offset duration = 67 ms, total adapter presentation time = 200 ms [three repetitions of 67 ms], and total duration of the adaptation trial = 600 ms). The orange bars correspond to Condition 4 (adapter's onset/offset duration = 67 ms, total adapter presentation time = 600 ms [nine repetitions of 67 ms], and total duration of the adaptation trial = 1,800 ms). Error bars correspond to the bootstrapped 95% confidence interval of the median of each duration condition. As illustrated, the conditions where the adapter's onset/offset duration was the same (67 ms) did not differ significantly from each other across numerosity stimuli.

In summary, we found that adaptation to a 600-ms adapter resulted in significantly different JND and PSE values when compared to adaptation to multiples of 67 ms, and when the adapter consisted of 40 or 80 but not 20 dots. In all cases, the duration conditions composed of multiples of 67 ms yielded similar—or at least not significantly different—JND and PSE values.

Table 1. *Post hoc comparisons using Wilcoxon signed-rank tests for an adapter and reference stimulus of 40 dots.*

	Conditions					
	67 ms vs 600 ms	67 ms vs 67 ms x 3	67 ms vs 67 ms x 9	600 ms vs 67 ms x 3	600 ms vs 67 ms x 9	67 ms x 3 vs 67 ms x 9
JND values						
Z	-3.30	-1.43	-1.68	-2.81	-2.81	-0.48
p	**0.01**	0.18	0.14	**0.01**	**0.01**	0.63
r	0.43			0.36	0.36	
PSE values						
Z	-3.24	-1.33	-1.27	-2.77	-2.71	-0.48
p	**0.01**	0.25	0.25	**0.01**	**0.01**	0.63
r	0.42			0.36	0.35	

Statistically significant *p* values are in bold (FDR-corrected).

Table 2. *Post hoc comparisons using Wilcoxon signed-rank tests for an adapter and reference stimulus of 80 dots.*

	Conditions					
	67 ms vs 600 ms	67 ms vs 67 ms x 3	67 ms vs 67 ms x 9	600 ms vs 67 ms x 3	600 ms vs 67 ms x 9	67 ms x 3 vs 67 ms x 9
JND values						
Z	-2.79	-0.36	-1.24	-2.89	-1.12	-1.74
p	**0.02**	0.72	0.31	**0.02**	0.31	0.16
r	0.36			0.37		
PSE values						
Z	-2.62	-0.20	-0.69	-2.81	-1.29	-1.47
p	**0.03**	0.85	0.59	**0.03**	0.30	0.28
r	0.34			0.36		

Statistically significant *p* values are in bold (FDR-corrected).

Adaptation of duration/numerosity channels yields similar effects on numerosity discrimination

Next we assessed which JND values were similar using Bayesian analyses. Our channel-based hypothesis predicts similar adaptation for identical onset/offset durations—that is, for the 67-ms adapter presentations. Whereas frequentist analyses focus on establishing whether two conditions are significantly different, Bayesian analyses can establish the probability that two conditions are similar.

The JND values obtained were examined by estimating a Bayes factor (BF) using Bayesian information criteria (Jarosz & Wiley, 2014; Wagenmakers, 2007), which compare the fit of the data under the alternative and the null hypothesis. We first performed a series of Bayesian paired-samples t tests comparing Conditions 1, 3, and 4, where the adapter's onset/offset duration was 67 ms (Figure 5, red lines).

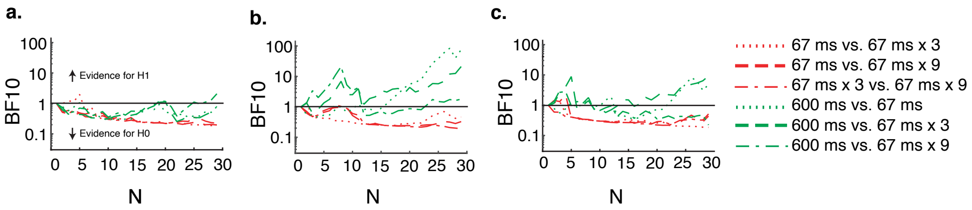

Figure 5. *Sequential-analysis plots for the Bayesian paired-samples comparisons in Experiment 1*. The plots display the flow of evidence for H_1 (just-noticeable differences in numerosity discrimination differ after adaptation to different duration conditions) versus H_0 (no difference in just-noticeable differences) as the data accumulate. The x-axis corresponds to the number of participants and the y-axis corresponds to the Bayes-factor values (ratios). The red lines correspond to the comparisons of Conditions 1, 3, and 4 with each other, where the adapter's onset/offset duration was 67 ms. The green lines correspond to the comparisons of Condition 2 (adapter's onset/offset duration: 600 ms = total duration of the adaptation trial) with Conditions 1, 3, and 4. (a) Using 20 dots as a visual duration adapter and reference stimulus, the evidence for H_1 (y-axis) decreases with the number of data points (x-axis) when Conditions 1, 3, and 4 are compared with each other. Comparing Condition 2 with Conditions 1 and 3, the evidence for H_1 decreases with the number of data points, whereas the evidence for H_1 increases in the comparison with Condition 4. (b) Using 40 dots as a visual duration adapter and reference stimulus, the evidence for H_1 decreases with the number of data points when Conditions 1, 3, and 4 are compared with each other. The opposite is true when Condition 2 is compared with Conditions 1, 3, and 4, where the evidence for H_1 increases. (c) Using 80 dots as a visual duration adapter and reference stimulus, the evidence for H_1 decreases with the number of data points when Conditions 1, 3, and 4 are compared with each other. The opposite is true when Condition 2 is compared with Conditions 1 and 3, where the evidence for H_1 increases, while it decreases in the comparison to Condition 4. These data suggest that the conditions which had the same onset/offset duration (67 ms) produced similar adaptation effects.

For Conditions 1 versus 3, 1 versus 4, and 3 versus 4, the BF_{10} was 0.20, 0.21, and 0.26, respectively, with an adapter and reference of 20 dots; and for 40 and 80 dots the BF_{10} was, respectively, 0.64, 0.39, 0.20 and 0.20, 0.56, and 0.56. This suggests that these data were less likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it. In other words, the aforementioned Bayes factors provide support for the notion that the JND values in Conditions 1, 3, and 4 are similar in all three conditions, which is in line with the duration/numerosity-channels hypothesis.

We then performed a series of Bayesian paired-samples *t* tests comparing Condition 2 (adapter's onset/offset duration: 600 ms = total duration of the adaptation trial: 600 ms) with Conditions 1, 3, and 4 (Figure 5, green lines). For Conditions 2 versus 1 and 2 versus 3, respectively, the BF_{10} was 0.80 and 0.71 for 20 dots. This suggests that these data were *less* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it. For 40 and 80 dots the BF_{10} was, respectively, 126.08 and 15.50, and 8.25 and 15.33, suggesting that these data were *more* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it.

For Condition 2 versus 4, the BF_{10} was 2.18 and 1.89, respectively, for 20 and 40 dots, suggesting that these data were slightly *more* likely to occur under the model including an effect, rather than the model without it. For 80 dots, the BF_{10} was 0.25, suggesting that these data were *less* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it. In general, Condition 2 differed from the other conditions, providing support for the duration/numerosity-channels hypothesis.

Based on the frequentist and Bayesian analyses we performed, these data suggest that the effect of adaptation to duration on numerosity discrimination was mainly driven by the onset/offset duration of the adapter, since Conditions 1, 3, and 4 (adapter's onset/offset duration = 67 ms) appeared similar to each other, while they were generally different from Condition 2 (adapter's onset/offset duration = 600 ms).

Total duration of adaptation affects numerosity discrimination after adaptation to numerosity (Experiment 2)

Similar to Experiment 1, we first examined which JND, PSE, and slope values differed using frequentist analyses. The JND and PSE values in almost all conditions were normally distributed. The two exceptions were the JND values obtained after adapting to a numerosity of 80 dots in Condition 4, as assessed by box plot and the Shapiro–Wilk test ($p = 0.003$), and the PSE values obtained using 80 dots as a visual duration adapter and reference stimulus in Condition 1 ($p = 0.013$). The slope values obtained were not normally distributed in the majority of conditions. Therefore, we used nonparametric statistical tests (Friedman and Wilcoxon signed-rank tests) for all comparisons. We corrected the significance thresholds using FDR correction where applicable (see Supplementary materials for the individual participants' data).

As seen in Figure 6a and 6b, there were statistically significant differences in the JND and PSE values in the four duration adaptation conditions after adaptation to numerosities of 20 dots, $\chi^2(3) = 22.95$, $p < 0.001$), 40 dots, $\chi^2(3) = 9.0$, $p = 0.03$, and 80 dots, $\chi^2(3) = 27.95$, $p <$

0.001 (see Tables 3–5 for post hoc comparisons). No statistically significant differences were found in the slope values after adapting to either 20, 40, or 80 dots—20: $\chi^2(3) = 3.45$, $p = 0.33$; 40: $\chi^2(3) = 4.25$, $p = 0.24$; 80: $\chi^2(3) = 7.25$, $p = 0.06$.

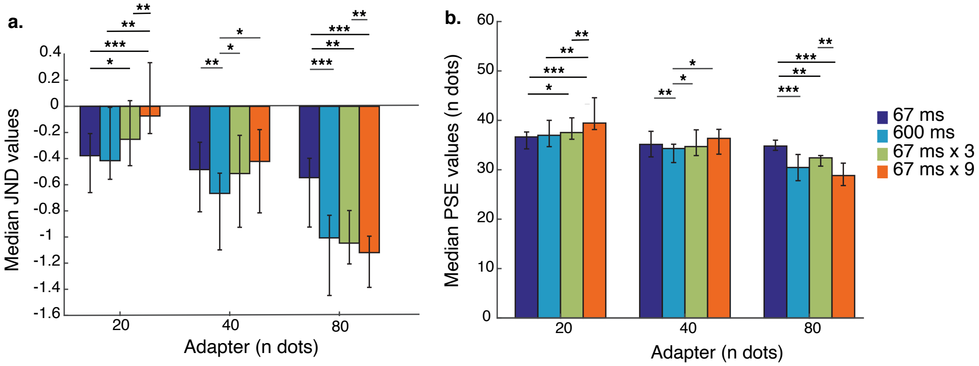

Figure 6. *(a) Median just-noticeable difference and (b) point of subjective equality for Experiment 2 (adaptation to numerosity and duration).* The x-axis displays the numerosity of the adapters (20, 40, or 80 dots). The y-axis displays the median just-noticeable difference or point of subjective equality obtained from the numerosity-discrimination task (the reference stimulus was always 40 dots). The colored bars correspond to the four duration adaptation conditions. The dark-blue bars correspond to Condition 1 (adapter's onset/offset duration: 67 ms = total duration of the adaptation trial). The bright-blue bars correspond to Condition 2 (adapter's onset/offset duration: 600 ms = total duration of the adaptation trial). The green bars correspond to Condition 3 (adapter's onset/offset duration = 67 ms, total adapter presentation time = 200 ms [three repetitions of 67 ms], and total duration of the adaptation trial = 600 ms). The orange bars correspond to Condition 4 (adapter's onset/offset duration = 67 ms, total adapter presentation time = 600 ms [nine repetitions of 67 ms], and total duration of the adaptation trial = 1,800 ms). Error bars correspond to the bootstrapped 95% confidence interval of the median of each duration condition. As illustrated, with adaptation to numerosity (20 and 80 dots), the condition where the total duration of the adaptation trial was the longest (1,800 ms) produced the strongest adaptation effects. In contrast, with adaptation to duration only (adapter and reference stimulus = 40 dots), the conditions where the adapter's onset/offset duration was the same (67 ms) did not differ significantly from each other (similar to Experiment 1).

Table 3. *Post hoc comparisons using Wilcoxon signed-rank tests for an adapter of 20 dots.*

	Conditions					
	67 ms vs 600 ms	67 ms vs 67 ms x 3	67 ms vs 67 ms x 9	600 ms vs 67 ms x 3	600 ms vs 67 ms x 9	67 ms x 3 vs 67 ms x 9
JND values						
Z	-1.63	-2.20	-3.77	-0.914	-3.11	-3.31
p	0.12	**0.04**	**0.001**	0.36	**0.004**	**0.003**
r		0.32	0.54		0.45	0.48
PSE values						
Z	-1.46	-2.20	-4.03	-0.97	-3.29	-3.46
p	0.17	**0.04**	**< 0.001**	0.33	**0.002**	**0.002**
r		0.32	0.58		0.47	0.50

Statistically significant *p* values are in bold (FDR-corrected).

Table 4. *Post hoc comparisons using Wilcoxon signed-rank tests for an adapter of 40 dots.*

	Conditions					
	67 ms vs 600 ms	67 ms vs 67 ms x 3	67 ms vs 67 ms x 9	600 ms vs 67 ms x 3	600 ms vs 67 ms x 9	67 ms x 3 vs 67 ms x 9
JND values						
Z	-3.26	-0.51	-0.49	-2.51	-2.43	-0.29
p	**0.01**	0.75	0.75	**0.03**	**0.03**	0.78
r	0.47			0.36	0.35	
PSE values						
Z	-3.14	-0.43	-0.29	-2.49	-2.49	-0.11
p	**0.01**	0.91	0.91	**0.03**	**0.03**	0.91
r	0.45			0.36	0.36	

Statistically significant *p* values are in bold (FDR-corrected).

In summary, we found that the strongest numerosity adaptation effects were produced under the duration condition which had the longest duration of the adaptation trial, even if the adapter's onset/offset duration was 67 ms. In contrast, in the case of adaptation to duration only (adapter and reference stimulus = 40 dots), the duration conditions composed of multiples of 67 ms yielded similar JND and PSE values (comparable to Experiment 1).

Table 5. *Post hoc comparisons using Wilcoxon signed-rank tests for an adapter of 80 dots.*

	Conditions					
	67 vs 600 ms	67 vs 67 x 3 ms	67 vs 67 x 9 ms	600 vs 67 x 3 ms	600 vs 67 x 9 ms	67 x 3 vs 67 x 9 ms
JND values						
Z	-3.60	-3.09	-4.00	-1.40	-1.49	-3.00
p	**0.001**	**0.004**	**< 0.001**	0.16	0.16	**0.005**
r	0.52	0.46	0.58			0.43
PSE values						
Z	-3.60	-2.97	-3.97	-1.63	-1.54	-3.20
p	**0.001**	**0.005**	**< 0.001**	0.12	0.12	**0.003**
r	0.52	0.43	0.57			0.46

Statistically significant *p* values are in bold (FDR-corrected).

Adaptation of duration/numerosity channels yields different effects on numerosity discrimination

Similar to Experiment 1, the JND values obtained were examined by estimating a Bayes factor using Bayesian information criteria (Figure 7, red lines).

For Conditions 1 versus 3, 1 versus 4, and 3 versus 4, the BF_{10} was, respectively, 3.94, 679.98, and 113.75 for an adapter and reference of 20 dots; and for 80 dots its was 30.14, 4,278, and 18.50. This suggests that these data were *more* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it. Thus, the aforementioned Bayes factors provide support for the notion that the JND values in Conditions 1, 3, and 4 are different.

Using an adapter of 40 dots, the BF_{10} for Conditions 1 versus 3, 1 versus 4, and 3 versus 4 was 0.35, 0.31, and 0.22, respectively, suggesting that these data were *less* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it.

We then performed a series of Bayesian paired-samples *t* tests comparing Condition 2 with Conditions 1, 3, and 4 (Figure 7, green lines).

For Condition 2 versus 1, the BF_{10} was 0.74 for 20 dots, suggesting that these data were *less* likely to occur under the model including an effect of adaptation to numerosity on numerosity discrimination, rather than the model without it.

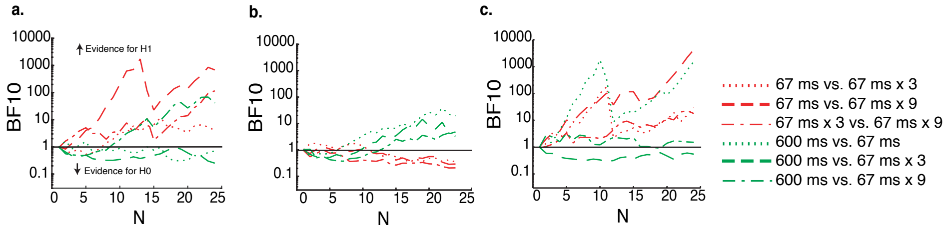

Figure 7. *Sequential-analysis plots for the Bayesian paired-samples comparisons in Experiment 2.* (a) Using 20 dots as a numerosity adapter, the evidence for H_1 (just-noticeable differences in numerosity discrimination differ after adaptation to numerosity and duration; y-axis) compared to H_0 (no difference in just-noticeable differences) increases with the number of data points (x-axis) when Conditions 1, 3, and 4 are compared with each other (red lines). When Condition 2 is compared with Conditions 1 and 3, the evidence for H_1 decreases with the number of data points, while the opposite is true when it is compared to Condition 4 (green lines). (b) Using 40 dots as a visual duration adapter and reference stimulus, the evidence for H_1 decreases with the number of data points when Conditions 1, 3, and 4 are compared with each other. The opposite is true when Condition 2 is compared with Conditions 1, 3, and 4, where the evidence for H_1 increases. Using 80 dots as a numerosity adapter, the evidence for H_1 increases with the number of data points when Conditions 1, 3, and 4 are compared with each other and when Condition 2 is compared with Condition 1. The trend is less definitive when Condition 2 is compared with Conditions 3 and 4. These data suggest that the conditions which had the same onset/offset duration produced different adaptation effects with adaptation to numerosity (adapter = 20 or 80 dots, reference stimulus = 40 dots) but not with adaptation to duration only (adapter and reference stimulus = 40 dots).

In contrast, for 40 and 80 dots the BF_{10} was 19.0 and 1,538, respectively, suggesting that these data were *more* likely to occur under the model including an effect of adaptation to numerosity on numerosity discrimination.

For Condition 2 versus 3, the BF_{10} was 0.27 and 0.56, respectively, for 20 and 80 dots, suggesting that these data were *less* likely to occur under the model including an effect of adaptation to numerosity on numerosity discrimination, rather than the model without it. In contrast, for 40 dots the BF_{10} was 4.76, suggesting that these data were *more* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it.

For Condition 2 versus 4, the BF_{10} was 40.53, 3.22, and 1.48, respectively, for 20, 40, and 80 dots, suggesting that these data were *more* likely to occur under the model including an effect of adaptation to duration on numerosity discrimination, rather than the model without it.

Based on the frequentist and Bayesian analyses we performed, these data suggest that in this experiment, the effect of adaptation to *numerosity* was mainly driven by the total duration of the adaptation trial. In contrast, the effect of adaptation to *duration* on numerosity discrimination (both adapter and reference stimulus = 40 dots; the same condition as in Experiment 1) was, again, mainly driven by the onset/offset duration of the adapter.

Validation of the numerosity aftereffect

We also examined whether adaptation to a low versus a high numerosity would lead to over- or underestimation, respectively, of the reference numerosity, in accordance with previous studies on adaptation to numerosity (see review by Anobile et al., 2016). We calculated the average JND, PSE, and slope values across duration conditions for each numerosity adaptation condition. There were statistically significant differences in both the JND and PSE after adaptation to numerosity, $\chi^2(2) = 24.33$, $p < 0.001$. Post hoc analysis with Wilcoxon signed-rank tests revealed that adaptation to a low numerosity (20 dots) led to significant overestimation of the reference numerosity ($\text{Mdn}_{\text{JND}} = -0.23$, $\text{Mdn}_{\text{PSE}} = 37.36$ dots) compared to the condition without numerosity adaptation (adapter and reference stimulus = 40 dots; $\text{Mdn}_{\text{JND}} = -0.50$, $\text{Mdn}_{\text{PSE}} = 35.46$ dots; both JND and PSE: $Z = -3.43$, $p = 0.001$, $r = 0.50$). In contrast, adaptation to a high numerosity (80 dots) led to significant underestimation of the reference numerosity compared to the condition without numerosity adaptation ($\text{Mdn}_{\text{JND}} = -0.93$, $\text{Mdn}_{\text{PSE}} = 31.59$ dots): The JND and PSE values were significantly lower compared to the condition without numerosity adaptation (JND: $Z = -3.06$, $p = 0.002$, $r = 0.44$; PSE: $Z = -3.69$, $p < 0.001$, $r = 0.53$). Moreover, adaptation to a low numerosity led to significant overestimation of the reference numerosity compared to adaptation to a high numerosity (JND: $Z = -4.26$, $p < 0.001$, $r = 0.61$; PSE: $Z = -4.11$, $p < 0.001$, $r = 0.59$).

In regard to the slope values, there were statistically significant differences after adaptation to numerosity, $\chi^2(2) = 7.58$, $p = 0.023$. Post hoc analysis with Wilcoxon signed-rank tests revealed that adaptation to a low numerosity (20 dots) led to significantly higher slope values (Mdn = 8.68 dots) compared to the condition without numerosity adaptation (Mdn = 7.96 dots), $Z = -2.46$, $p = 0.04$, $r = 0.36$. No other significant differences were found.

These findings show that adapting to a low versus a high numerosity leads to overestimation versus underestimation of the reference numerosity, respectively, compared to the condition without numerosity adaptation.

Control experiment on the role of a time-order effect

In both experiments, there was a general underestimation in the numerosity-discrimination task which could be explained by a negative time-order effect (TOE). Specifically, when two stimuli are being discriminated, the stimulus presented last is judged as being of a greater magnitude, corresponding to a negative TOE.

In order to elucidate this further, we performed a control experiment with five individuals (four of whom were the authors). Specifically, we used an adapter and reference stimulus of 40 dots (the same condition as in Experiments 1 and 2) and two durations (67 vs. 600 ms). We introduced four adaptation conditions (Figure 8, left to right; see also Supplementary materials for the individual participants' data).

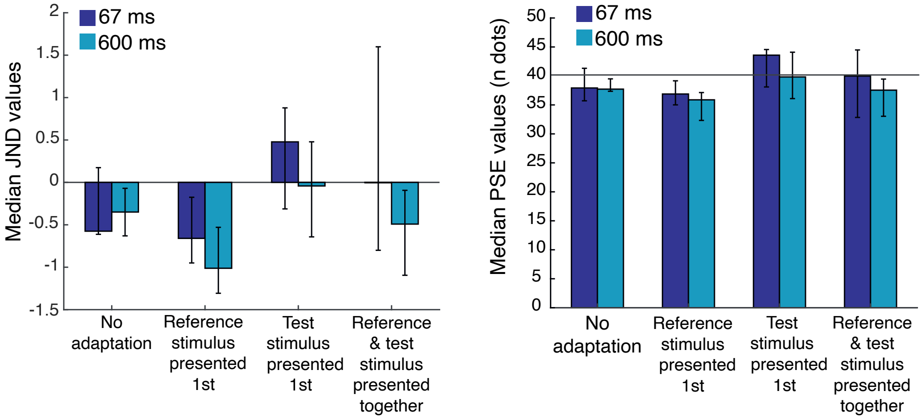

Figure 8. *(a) Median just-noticeable difference and (b) point of subjective equality across participants (N = 5) for the control experiment.* Error bars correspond to the bootstrapped 95% confidence interval of the median of each condition. Irrespective of presentation-order condition, adaptation to a long onset/offset duration (600 ms; light-blue bars) resulted in lower just-noticeable differences and points of subjective equality (i.e., underestimation of reference numerosity) compared to adaptation to a short onset/offset duration (67 ms; dark-blue bars).

In Condition 1, there was no visual adapter stimulus. The reference stimulus appeared on the left of the fixation cross and after an ISI, the test appeared on the opposite side (the sides switched after 50% of the trials were complete). Condition 2 was the same as in Experiments 1 and 2 (adapter and reference = 40 dots). In Condition 3, the test stimulus appeared first (opposite side of the adapter), and after an ISI the reference stimulus appeared on the side of the adapter. In Condition 4, the reference and test stimulus appeared simultaneously (again, at opposite sides of the fixation cross), after the adapter was presented.

Based on the data shown in Figure 8, in the case of no visual adaptation there is again a general underestimation of the reference stimulus (67 ms: $\mathrm{Mdn}_{\mathrm{JND}} = -0.58$, $\mathrm{Mdn}_{\mathrm{PSE}} = 37.92$ dots; 600 ms: $\mathrm{Mdn}_{\mathrm{JND}} = -0.35$, $\mathrm{Mdn}_{\mathrm{PSE}} = 37.72$ dots), similar to Condition 2 (67 ms: $\mathrm{Mdn}_{\mathrm{JND}} = -0.66$, $\mathrm{Mdn}_{\mathrm{PSE}} = 36.88$ dots; 600 ms: $\mathrm{Mdn}_{\mathrm{JND}} = -1.01$, $\mathrm{Mdn}_{\mathrm{PSE}} = 35.88$ dots) and as found in Experiments 1 and 2. This could point to a general response bias, which could indeed derive from a TOE, with the test stimulus presented last being consistently judged as more numerous. In regard to Condition 3 (reference stimulus presented last; 67 ms: $\mathrm{Mdn}_{\mathrm{JND}}$ = 0.48, $\mathrm{Mdn}_{\mathrm{PSE}}$ = 43.59 dots; 600 ms: $\mathrm{Mdn}_{\mathrm{JND}}$ = –0.04, $\mathrm{Mdn}_{\mathrm{PSE}}$ = 39.82 dots) and Condition 4 (reference and test stimulus presented simultaneously; 67 ms: $\mathrm{Mdn}_{\mathrm{JND}}$ = –0.003, $\mathrm{Mdn}_{\mathrm{PSE}}$ = 39.98 dots; 600 ms: $\mathrm{Mdn}_{\mathrm{JND}}$ = –0.49, $\mathrm{Mdn}_{\mathrm{PSE}}$ = 37.55 dots), there is a trend for JND and PSE values to be higher when adapting to a short duration, which is not the case in Conditions 1 and 2. This difference could confirm that the general underestimation we found in our reported experiments is an outcome of a TOE.

However, if the explanation for our findings about the effect of adaptation to duration on numerosity perception is that it is merely an outcome of a TOE, then adapting to a long duration (600 ms; Conditions 3 and 4) would not lead to underestimation of the reference stimulus, and the two duration conditions would yield similar JND and PSE values. So overall, the order of the stimulus presentation appears to matter, but it does not explain why adapting to a short versus a long onset/offset duration leads to differences in the JND and PSE values, or the differential effect of duration we found in Experiments 1 and 2.

5. Discussion

We have previously shown that adaptation to duration alters numerosity perception (Tsouli, Dumoulin, et al., 2019). Here we examined *how* it influences numerosity perception. In addition, we examined whether the nature of that effect would be similar when adapting to duration only and when adapting to numerosity as well. In both experiments, we hypothesized that if the influence of duration on numerosity perception is driven by the adaptation of duration/numerosity channels tuned to specific durations/numerosities, then the conditions where the adapter's onset/offset duration was the same (67 ms) would produce similar adaptation effects. On the other hand, if the effect of duration on numerosity perception is driven by the strength of adaptation of numerosity-selective channels only (i.e., the longer the adaptation period, the stronger the perceptual aftereffects), then the conditions where the adapter's total presentation time or the total duration of the adaptation trial was longest (i.e., 600 or 1,800 ms) would produce the strongest adaptation effects. However, the hypotheses are not mutually exclusive.

Using both frequentist and Bayesian analyses, we found that the JND and PSE values on the duration adaptation conditions where the adapter's onset/offset duration was the same (multiple presentations of 67 ms) were generally similar and differed from the duration adaptation condition where the adapter's onset/offset duration was different (600 ms). These results support the channel-based hypothesis—that is, the effect of adaptation to duration on numerosity discrimination is driven by duration channels encoding the onset/offset duration of an event, and not the adapter's total presentation duration or the total duration of the adaptation trial. These onset/offset duration channels could also encode numerosity or wire together with numerosity channels (duration/numerosity channels). Specifically, adaptation to a long onset/offset duration (i.e., 600 ms) induced the same adaptation effect as would adaptation to a high numerosity (e.g., 80 dots). This finding was further replicated in Experiment 2. By contrast, when we induced adaptation to numerosity *and* to duration, our overall finding was that the condition with the longest total duration of the adaptation trial (i.e., 1,800 ms) produced the strongest perceptual aftereffects, even if the onset/offset duration of the adapter was short (i.e., 67 ms). Hence, the strength-of-adaptation hypothesis appears to capture the effect of duration when adapting to numerosity *and* duration.

Theoretical implications

Based on these findings, a number of theoretical inferences arise. First of all, we have successfully replicated the finding that adaptation to duration affects numerosity perception in both of our experiments (Tsouli, Dumoulin, et al., 2019). This could to some extent support the theories which suggest that temporal and numerical representations share computation mechanisms and possibly neural resources (Bueti & Walsh, 2009; Cantlon et al., 2009; Cappelletti, Freeman, & Cipolotti, 2011; Walsh, 2003).

The novel finding of our study is that the effect of adaptation to duration on numerosity perception appears to be driven by the adaptation of duration channels tuned to the onset/offset duration of the adapter. This channel-based hypothesis is in line with numerosity-tuned neural populations (Harvey et al., 2013, 2015; Harvey & Dumoulin, 2017a; Nieder et al., 2002; Nieder & Miller, 2004a; Viswanathan & Nieder, 2013; Wagener et al., 2018) and duration-tuned neural populations (Aubie et al., 2012; Becker & Rasmussen, 2007; Duysens et al., 1996; Hawken et al., 1996; Heron, Aaen-Stockdale, et al., 2012; Leon & Shadlen, 2003; Maarseveen et al., 2019; Mita et al., 2009), with our results implying either that onset/offset duration channels also encode numerosity or that there is neuronal communication between duration-selective and numerosity-selective channels (duration/numerosity channels).

Our second experiment reveals a very different pattern of the numerosity–time interaction. We found that the duration condition with the longest total duration of the adaptation trial (1,800 ms) produced the strongest perceptual aftereffects, even if the adapter's onset/offset duration was very short (67 ms). Based on this, we speculate that in the context of adaptation to numerosity, the influence of time can be explained by the strength of adaptation of numerosity-selective channels only, without the involvement of duration/numerosity channels. Thus, longer adaptation periods result in stronger perceptual aftereffects similar to adaptation effects for other visual features (Dragoi et al., 2000; Magnussen & Johnsen, 1986).

The role of the total duration of the adaptation trial we found in our study is seemingly at odds with the study of Aagten-Murphy and Burr (2016), who found that the numerosity aftereffect is driven by the number of trials or events, not by the duration of the numerosity adapter. However, we argue that indeed, the strongest perceptual aftereffects could result from the number of adaptation events or the frequency of visual events. More specifically, the duration condition with the longest total duration of the adaptation trial (1,800 ms) was composed of nine repetitions of 67 ms, which was the largest number of repetitions among all duration conditions and also had the highest frequency of events. Hence, we suggest that what could be considered an adaptation event is not only the number of trials but the number of repetitions of the adapter stimulus within a single adaptation trial, and also the frequency of events, regardless of the onset/offset duration of the adapter. Our finding that the strongest perceptual aftereffects are obtained with a repeated presentation of the adapter within the same trial, even with a very short adapter onset/offset duration, could serve as a methodological parameter for future numerosity adaptation experiments.

All in all, we speculate that the two demonstrated adaptation phenomena (one based on adapted duration/numerosity channels, the other on adapted numerosity channels only) might be governed by partially distinct neuronal populations. Such a speculation is in accordance with a number of neuroimaging studies revealing a number of different brain regions involved in time perception (Ferrandez et al., 2003; Harrington et al., 1998; Hayashi et al., 2014; Pouthas et al., 2005), which do not always overlap with the brain regions involved in numerosity perception (Dormal et al., 2008; Harvey et al., 2013; Harvey & Dumoulin, 2017a). From examining neuroimaging studies that use an adaptation paradigm, the supramarginal gyrus appears to be involved in adaptation to duration (Hayashi et al., 2015), whereas the intraparietal sulcus appears to be involved in adaptation to numerosity (Castaldi et al., 2016). Therefore, we suggest that further functional neuroimaging studies could perhaps confirm our hypothesis that there are at least partially dissociable activations when examining the effect of *adaptation to duration* on numerosity perception, compared to the effect of the *duration of adaptation* on numerosity perception.

Multiple temporal mechanisms further imply that there are multiple duration mechanisms rather than a single, supramodal timing mechanism (Bruno & Cicchini, 2016; Ivry, 1996; Motala et al., 2018). Such an interpretation could mean that there are less specialized duration mechanisms interacting with different magnitudes, such as numerosity and space, as the ATOM theory suggests (Bueti & Walsh, 2009; Walsh, 2003), and other, more specialized duration mechanisms dedicated for duration processing only. This distinction could also explain the contradicting findings from (behavioral) studies examining the interaction of time and numerosity (Chun et al., 2018; Javadi et al., 2014; Javadi & Aichelburg, 2012; Lambrechts et al., 2013; Martin et al., 2017; Tsouli, Dumoulin, et al., 2019).

In regard to the predictions of ATOM (Bueti & Walsh, 2009; Walsh, 2003), we also hypothesized that if numerosity and time are indeed part of a common magnitude system, then low versus high numerosities could be perceptually associated with short versus long durations. Hence, in the context of adaptation to numerosity, adapting to, for example, a low numerosity using a short duration should produce greater overestimation of the reference numerosity. We did not find support for this postulation in our second experiment, at least when examining the combination of low numerical and temporal magnitudes. More specifically, adapting to a low numerosity (20 dots) using a short duration (67 ms; Condition 1) did not result in greater overestimation of the reference numerosity compared to the conditions with a longer duration. However, we do not know the exact perceptual correspondence of numerical and temporal magnitudes (e.g., whether 67 ms is perceptually associated with 20 dots) which could account for this discrepancy.

Further considerations

When we used a high numerosity (80 dots), it appeared that the conditions with the longest total adapter presentation time (600 ms; i.e., Conditions 2 and 4) did not differ significantly from each other in either experiment. Hence, the total adapter presentation time (600 ms) appeared to drive the effect of adaptation to duration, as well as adaptation to numerosity *and* duration, with a high-numerosity stimulus. This could imply different mechanisms for the interaction of time and numerosity, which could be modulated by not only duration channels tuned to specific durations but also numerosity channels tuned to specific numerosities. In addition, given that the size of the dot stimuli was kept constant across numerosities, it is possible that density-processing mechanisms which are more pronounced with a high-numerosity stimulus could have played a role (Dakin et al., 2011; Durgin, 2008). Nevertheless, the conditions where the adapter's onset/offset duration was the same (67 ms) did not differ from each other in the first experiment, whereas they did in the second. This is in agreement with the hypothesis on the adaptation of duration/numerosity channels.

When we examine the overall effect of adaptation, the JND and PSE values we report show a general underestimation. We believe that this can be explained in terms of a time-order effect (TOE), according to which comparison judgments can be affected by the spatial or temporal separation between the compared stimuli (Fechner, 1860; Needham, 1934). More specifically, in the presence of a negative TOE, when two stimuli are being discriminated, the stimulus presented last is judged as being of a greater magnitude. Recently, it has been shown that nonsymbolic numerosity comparisons are affected by a negative TOE (van den Berg et al., 2017). Indeed, in our study the test stimulus was always presented last, which could mean that it was more frequently judged as more numerous, leading to underestimation of the reference stimulus. In order to examine the potential role of a TOE and its association with numerosity perception in our experiments, we performed a control experiment. Overall, we found that a negative TOE could at least partially explain the underestimation. Importantly, regardless of the underestimation, the results produced by the adaptation conditions still supported the differential effects of adaptation to a short versus a long duration.

Another finding of our first experiment, on adaptation to duration, was the lower JND and PSE values obtained when the adapter and reference stimulus were presented on the left compared to the right side of the screen, across duration and numerosity conditions. This difference could be interpreted as an extension of the spatial-numerical association of response codes, in which shorter reaction times are recorded when low numbers are presented to the left and high numbers are presented to the right (Cohen Kadosh et al., 2008; Dehaene et al., 1993). This effect is thought to derive from an introspective association of numbers with spatial locations and the so-called mental number line, where low numbers are associated with the left side and high numbers with the right side (Dehaene et al., 1993). While the effect is well documented in examination of symbolic numerosities (e.g., Arabic numerals), recent evidence shows that the perception of nonsymbolic numerosities (e.g., arrays of dots) can also be affected by spatial manipulations (Fornaciai et al., 2018; Liu et al., 2015; Nemeh et al., 2018; Schwiedrzik et al., 2016). Hence, the underestimation of numerosities presented on the left side that we found in our first experiment could be an outcome of the aforementioned mental number line, with participants perceiving numerosities presented on the left as generally lower. Nevertheless, we are cautious in endorsing this finding, since we found no such difference in our second experiment nor in our previous research on numerosity and duration adaptation (Tsouli, Dumoulin, et al., 2019).

Conclusions

We found that adaptation to duration affects numerosity perception by adapting onset/offset-duration channels which also encode numerosity or wire together with numerosity-selective channels. This finding is in agreement with the channel-based hypothesis on the interaction of duration and numerosity. When examining the role of duration on adaptation to numerosity, we found that the numerosity aftereffects were driven by the total duration of the adaptation trial, not by the onset/offset duration of the adapter. This finding appears to support the strength-of-adaptation hypothesis, where only numerosity channels are adapted. We propose that different temporal mechanisms are involved in adaptation to duration compared to adaptation to numerosity.

Chapter 5

The role of neural tuning in quantity perception

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Abstract

Perception of quantities, such as numerosity, timing, and size, is essential for behavior and cognition. Accumulating evidence demonstrates neurons processing quantities are tuned, that is, have a preferred quantity amount, not only for numerosity, but also other quantity dimensions and sensory modalities. We argue that quantity-tuned neurons are fundamental to understanding quantity perception. We illustrate how the properties of quantity-tuned neurons can underlie a range of perceptual phenomena. Furthermore, quantity-tuned neurons are organized in distinct but overlapping topographic maps. We suggest that this overlap in tuning provides the neural basis for perceptual interactions between different quantities, without the need for a common neural representational code.

Neural tuning as the basis of quantity perception

Quantity perception refers to the ability to seemingly effortlessly sense the amount or quantity of sensory information. Both humans and animals can readily judge discrete quantities, such as numerosity, that is, the set size of a group of items, and use this information to make decisions, such as choosing the tree with the most fruit (Nieder, 2021). This ability is also present for continuous quantity dimensions, such as event timing and object size. This intuitive understanding of quantities is crucial for navigating the world, exploiting food sources and avoiding predation (Nieder, 2020b).

The neural and perceptual basis of quantity perception have been studied extensively in recent decades, using psychophysics, neuroimaging, and neurophysiology, in humans, nonhuman primates, birds, fish, and insects. In addition, many perceptual interactions between different dimensions of quantity and different sensory modalities have been demonstrated (Arrighi et al., 2014; Bonn & Cantlon, 2012; Cantlon et al., 2009; Church & Broadbent, 1990; Cohen Kadosh et al., 2008; Gallistel & Gelman, 2000; Walsh, 2003). However, how the neural representation of quantities gives rise to perception remains elusive.

In this opinion article, we show that neural tuning is at the core of the neural representation of quantity and propose that this neural tuning is critical to understanding quantity perception. The idea that neural tuning is linked to perception is not new (Kersey & Cantlon, 2017; Lasne et al., 2019; Nieder, 2020a; Nieder & Dehaene, 2009; Nieder & Miller, 2004b), and is well established in vision and perception in general. However, recent developments highlight the ubiquitous nature of neural tuning in quantity systems; for example, discoveries of neural tuning for different quantity dimensions and modalities, and the topographic organization of quantity-tuned neural populations. Guided by these new insights and the established links between neural tuning and perception in sensory cortices, we illustrate how neural tuning can account for various perceptual phenomena in quantity perception, including the numerical distance and size effect, the subitizing and estimation ranges, and adaptation effects. We further propose that perceptual interactions between different quantities and modalities result from interactions between spatially intermixed, topographically organized neural populations tuned to different quantities and modalities.

Neural tuning and perception

Neural tuning and topographic maps are fundamental properties of primary sensory and motor cortices. For example, the visual cortex projects the retinal image onto the cortical surface in visual field maps that contain neurons tuned to specific locations of the visual field constituting their receptive fields (Wandell et al., 2007). Likewise, the auditory cortex maps the cochlea's auditory frequency-specific responses (tonotopy), while somatosensory and motor cortices map the body's layout (somatotopy) (Penfield & Boldrey, 1937).

Neural tuning and topographic organization of visual cortical neurons are closely linked to perception (Penfield & Boldrey, 1937). Damage or electrically stimulating specific parts of the early visual cortex causes blindness (Holmes, 1918; Inouye, 1909) or perceived flashes (Brindley & Lewin, 1968) respectively at the corresponding visual location. Furthermore, the properties of these maps match perception: in the visual cortex, more neurons, with sharper tuning, respond to a stimulus in the central than in the peripheral visual field, giving more detailed visual perception centrally (Holmes, 1918; Inouye, 1909). Similar relationships occur in all other primary sensory and motor cortices (Saenz & Langers, 2014; Schieber, 2001).

Neural tuning is not limited to locations on sensory or motor organs, like retinal position. For example, visual neurons are also tuned to specific orientations (Hubel & Wiesel, 1968), spatial frequencies (De Valois et al., 1982) and motion directions (Dubner & Zeki, 1971). Perception of these features depends on the activity of correspondingly tuned neurons, and stimulating these neurons biases perception towards their tuning preferences (Blakemore & Cooper, 1970; DeAngelis et al., 1998; Romo et al., 1998; Salzman et al., 1990). Thus, in sensory cortices, the proposal that neural tuning underlies perception is supported by extensive evidence collected over the past century.

Neural tuning in visual numerosity processing

Analogous to neurons in early sensory cortices, neurons exist that are tuned to quantities, such as visual numerosity (Nieder et al., 2002). The responses of numerosity-selective neurons peak when a specific numerosity is presented (the preferred numerosity), with different neurons exhibiting different preferred numerosities. Responses decrease with increasing difference between the presented and preferred numerosity, commonly modeled using a logarithmic Gaussian function (Dehaene, 2001b; Dehaene & Changeux, 1993; Nieder & Miller, 2003) (Figure 1A,B). On a linear scale, numerosity tuning curves are asymmetrical, and increase in tuning width (the numerosity range to which these neurons respond) as the preferred numerosity increases (Figure 1A). On a logarithmic scale, numerosity tuning curves become symmetrical with constant tuning width across numerosities (Figure 1B).

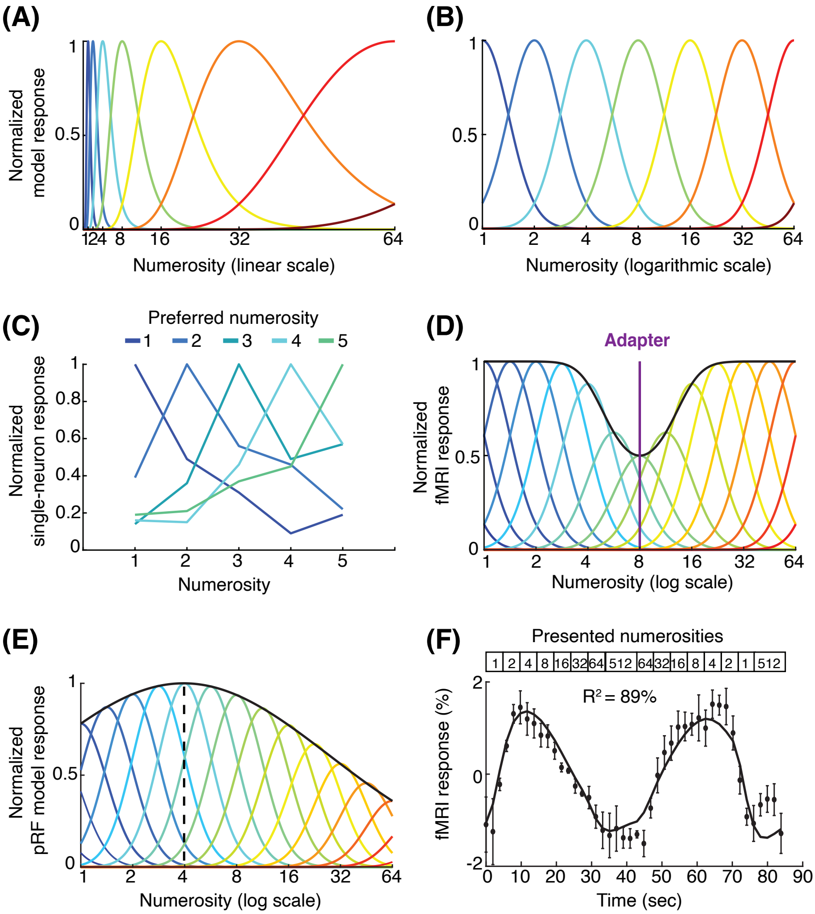


Figure 1. *Characterizing numerosity-tuned neurons.* (A) Numerosity-selective neurons are typically modeled as logarithmic Gaussian functions. The colors represent tuning curves with different preferred numerosities. On a linear scale, tuning curves are asymmetric and increase in width with preferred numerosity. (B) When plotted on a logarithmic scale, the model tuning curves become symmetric with a constant tuning width across different numerosities. (C) Single-neuron responses in macaque parietal cortex reveal that different neurons prefer, or are tuned to, different numerosities (drawn after: Nieder & Miller, 2004a). (D) Functional magnetic resonance imaging (fMRI) responses are attenuated during fMRI adaptation, where fMRI response amplitudes are reduced depending on the distance between adapter and test stimuli (black line) (inspired by: Piazza et al., 2004). The colors indicate the hypothesized single-neuron tuning functions underlying the fMRI response. (E) Population receptive field (pRF) models summarize the aggregate responses of tuned neural populations within a cortical location (solid black line) (Dumoulin & Wandell, 2008). The dashed line indicates the preferred numerosity of the neural population, whereas the colored lines indicate the hypothesized, underlying single-neuron contributions to the population responses. (F) Example of a parietal cortical location's fMRI time course (points: mean response amplitude; error bars: standard error over repeated measurements) elicited by viewing a sequence of numerosity stimuli (top) (data from: Cai et al., 2021). The solid line shows the responses predicted by the pRF model from panel E. Here, the response amplitude peaks after the presentation of numerosity 4. These different approaches provide converging evidence that neurons are tuned to numerosity.

The characterization of neurons tuned to visual numerosity was first made using single-cell recordings in nonhuman primates (Nieder et al., 2002; Nieder & Miller, 2003, 2004a) (Figure 1C) and more recently in humans (Kutter et al., 2018). Human single-cell recordings are rare and converging evidence of neurons tuned to numerosity in humans has been provided using functional magnetic resonance imaging (fMRI). FMRI typically measures changes in blood flow and oxygenation that follow neural activity (Logothetis & Wandell, 2004).

Numerosity tuning in humans was first shown using fMRI adaptation (Piazza et al., 2004). FMRI adaptation infers neural tuning is present because of decreased fMRI responses to a specific test numerosity after repeated presentation of another adapter numerosity. When the suppression of responses systematically decreases with the difference between adapter and test numerosity, this implies neural tuning (Figure 1D). In other words, adaptation affects neural populations depending on their numerosity tuning, where neural populations' responses are suppressed based on their shared response to the adapter and test numerosity.

Recently, visual numerosity tuning has also been measured by combining ultra-high field fMRI (Cai, Hofstetter, van der Zwaag, et al., 2021; Cai, Hofstetter, van Dijk, et al., 2021; Harvey et al., 2013; Harvey & Dumoulin, 2017a, 2017b) with biologically inspired neural model-based analyses [population receptive field (pRF) modeling] (Dumoulin & Wandell, 2008). PRF modeling summarizes responses to many presented numerosities using tuning functions (Figure 1E) by comparing the prediction of how many candidate tuning functions would respond to the presented numerosities against the responses measured at each cortical location (Figure 1F). The candidate tuning function that generates the prediction best correlated to a cortical location's measured response is taken as the tuning function of the neural population at that location.

The studies using this method not only demonstrated neural tuning but uncovered the organization of tuned neural populations in networks of topographic maps, where preferred numerosity varies systematically across the cortex akin to a mental number line (Harvey et al., 2013; Harvey & Dumoulin, 2017a, 2017b). Many other neuroimaging studies are also consistent with the existence of topographically organized numerosity-tuned neurons, for example those using multivoxel pattern analysis (Bulthé et al., 2014; Cavdaroglu & Knops, 2019; Eger et al., 2009) and representational similarity analysis (Castaldi et al., 2019). These converging results suggest that topographic principles common in primary sensory and motor cortices are also an organizational principle of quantity mechanisms in the brain.

One alternative view proposes that numerosity tuning and perception reflect non-numerical image features that are often correlated with numerosity, such as density or surface area (Leibovich et al., 2017). However, growing convergent evidence from psychophysical (Cicchini et al., 2016; DeWind et al., 2015), neuroimaging and computational research (Harvey & Dumoulin, 2017a, 2017b, 2018) indicates numerosity itself is represented and perceived. This is further supported by recent computational research using neural network models which show numerosity-tuned responses (Nasr et al., 2019; Zorzi & Testolin, 2018) even in networks with no training (Kim et al., 2021; Testolin et al., 2020). Thus, a growing body of neuroscientific evidence supports the existence of a specialized neural system processing numerosity and that numerosity-tuned neurons are the core of this network.

Neural tuning underlies visual numerosity perception

Akin to the fact that neural tuning underlies primary sensory perception, established behavioral effects in numerosity perception can be explained by the properties of numerosity tuning functions. We highlight the tuning functions for numerosities 3, 4, 8, and 9, for illustration purposes (Figure 2A,B). Specifically, we discuss the numerical distance and size effects, subitizing and estimation, and adaptation.

Humans and animals show similar patterns of numerosity perception that obey Weber's law (Cantlon & Brannon, 2006; Cheyette & Piantadosi, 2020; Ditz & Nieder, 2016). Specifically, behavioral discrimination improves with increasing numerical distance (numerical distance effect) and discrimination between two quantities with equal numerical distance deteriorates as their numerical size increases (numerical size effect) (Buckley & Gillman, 1974) (Figure 2C). Following Weber's law, the discrimination threshold between two numerical stimuli increases with numerosity of the stimuli: as numerosities increase, a larger difference between them is necessary for a fixed discrimination performance. This difference is proportional to the discriminated numerosities. Therefore, in the numerical distance effect, more numerically distant numerosities (e.g., 4 vs 8) are easier to discriminate than close numerosities (e.g., 8 vs 9). In the numerical size effect, two numerosities of a given numerical distance are easier to discriminate when the numerosities are lower (e.g., 3 vs 4) than when they are higher (e.g., 8 vs 9). Hence, in both the numerical distance and size effects behavioral discrimination performance will increase as a function of the ratio of compared numerosities (Halberda & Feigenson, 2008) (Figure 2D).

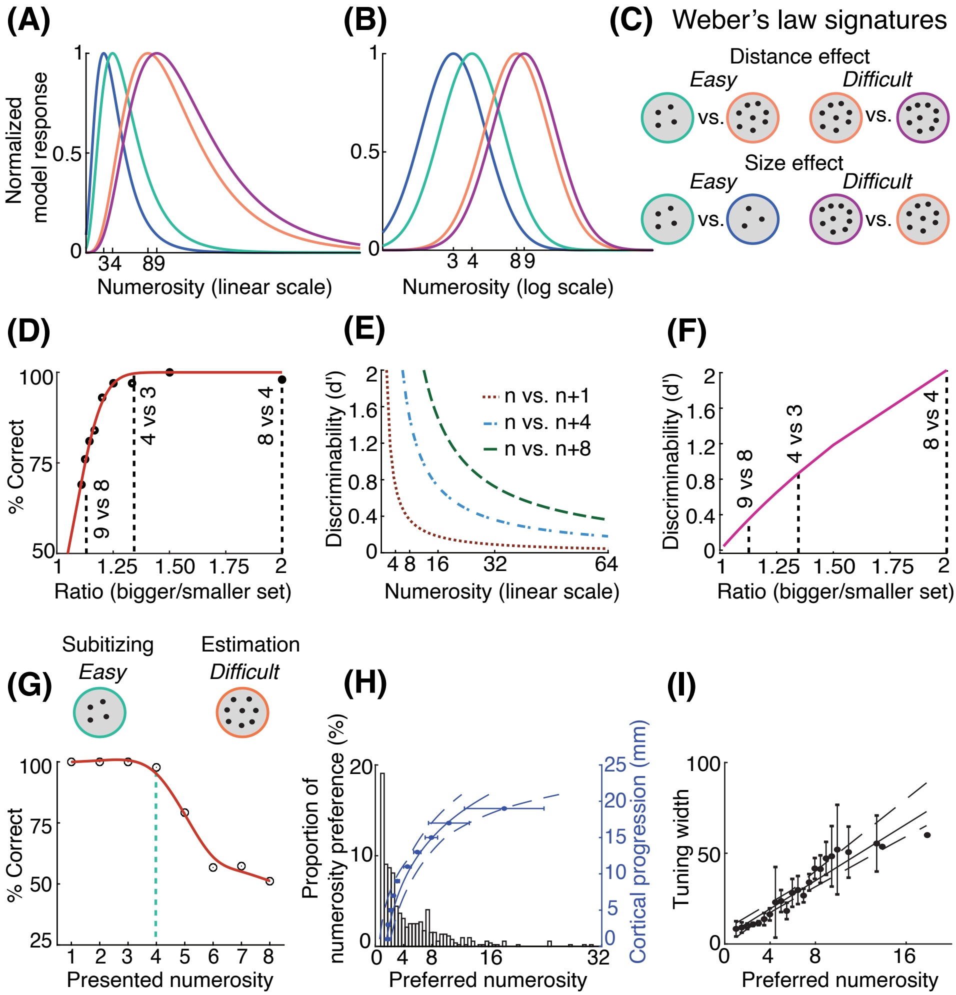


Figure 2. *Numerosity tuning functions account for perceptual effects.* (A) Idealized numerosity tuning functions with a preferred numerosity of 3, 4, 8, and 9 on a linear and (B) logarithmic scale. (C) Two numerosity perception effects reflecting Weber's law. The numerical distance effect: easier discrimination of distant numerosities (e.g., 4 vs 8) than closer numerosities (e.g. 8 vs 9). The numerical size effect: easier discrimination of low (e.g., 3 vs 4) than high numerosities (8 vs 9) at a given numerical distance (1 here). (D) In both effects, discrimination improves as the ratio of compared numerosities increases (drawn after: Halberda & Feigenson, 2008). (E) Using a signal detection framework, the discriminability index (d′) is lower with more overlapping tuning functions. Discriminability is higher when any numerosity n is compared against a more different numerosity (n+8) than a more similar numerosity (n+1) (distance effect), and decreases with increasing numerosity (size effect). (F) In both the size and distance effect, discriminability increases following the ratio of compared numerosities. (G) Enumeration of up to four items (subitizing) is error free, while enumeration of higher numerosities (estimation) is error prone (drawn after: Revkin et al., 2008). This discrepancy between subitizing and estimation may reflect neural tuning properties (H, I). (H) Preferred numerosities progress continuously along the cortex covering both ranges, but more cortical area (blue) and more neural populations (black) respond to lower numerosities (data from: Cai, Hofstetter, van Dijk, et al., 2021). Blue lines show

logarithmic fit with 95% confidence intervals (dashed lines). (I) Neural tuning width increases with preferred numerosity (data from: Cai, Hofstetter, van Dijk, et al., 2021). Points in (H) and (I) represent the mean and standard error of the mean.

Both numerical distance and size effects can be attributed to the response functions of the underlying numerosity-tuned neurons (Nieder, 2016; Nieder & Dehaene, 2009). The response functions of neurons preferring 8 and 9 overlap more than those preferring 4 and 8, making these neural responses more similar and less discriminable, mirroring the numerical distance effect (Figure 2A,B). Moreover, numerosity response functions become progressively wider with increasing numerosity, so that the same numerical difference (a difference of 1; 3 vs 4 and 8 vs 9; Figure 2A,B) produces more overlapping response functions as numerosity increases. This reflects the numerical size effect. More generally, under the signal detection framework, the observer's discrimination performance depends on the degree of overlap between response functions. Therefore, in the numerical distance effect, the discriminability index (d′) will be lower with a small numerical distance and more overlap between response functions (e.g., *n* versus *n* + 1; Figure 2E), and higher with a large numerical distance and less overlap between response functions (e.g. *n* vs *n* + 8; Figure 2E). Similarly, in the numerical size effect, for a fixed numerical distance, the discriminability index will be higher at low numerosities and lower at high numerosities (Figure 2E). Uniting both effects, the discriminability index will increase as a function of the ratio of compared numerosities (Figure 2F), akin to behavioral observations (Halberda & Feigenson, 2008) (Figure 2D).

Another well-documented behavioral phenomenon is the fast and error-free perception of very low numerosities (up to four items), known as subitizing (Kaufman et al., 1949). The subitizing range is thought to be distinct from higher numerosities (Anobile et al., 2016; Feigenson et al., 2004; Kaufman et al., 1949), primarily due to evidence for discontinuous behavioral performances observed in reaction time and accuracy (Revkin et al., 2008) (Figure 2G). For example, response variability in numerosity judgements is much lower in the subitizing range (Revkin et al., 2008). The discontinuous behavioral performances are a violation of Weber's law (Revkin et al., 2008). Further evidence suggests that subitizing depends on attentional resources, more than estimation at higher numerosities (Anobile et al., 2012; Burr et al., 2010). Last, subitizing could also be a result of educational experience, which may explain why there is no apparent precision change in enumerating very low compared to higher numerosities in animals (Cantlon & Brannon, 2006; Ditz & Nieder, 2016; Nieder & Merten, 2007; Nieder & Miller, 2004b), and why innumerate adults have difficulty processing even set sizes smaller than three items on more cognitively demanding numerical tasks (Gordon, 2004).

However, the notion of separate numerosity systems for subitizing and estimation is not universally accepted (Cheyette & Piantadosi, 2020; van Oeffelen & Vos, 1982). Studies examining numerosity tuning show that numerosity-selective neurons respond to low and high numerosities with similar tuning functions (Ditz & Nieder, 2016; Nieder & Merten, 2007; Nieder & Miller, 2004b; Piazza et al., 2004). Furthermore, the effect of attention appears to be in proportion to the respective difficulty of enumerating both subitizing and estimation ranges, suggesting that subitizing and estimation are *equally* affected and may therefore still rely on a single mechanism (Vetter et al., 2008). Last, innumerate adults *can* subitize (Everett & Madora, 2012; Gordon, 2004), arguing against a role of education in subitizing.

Recently, we demonstrated a continuous neural representation of subitizing and estimation range numerosity preferences within the same numerosity maps (Cai, Hofstetter, van Dijk, et al., 2021). In other words, as one travels along the cortex, there is a progression of numerosity preferences that seamlessly traverses from subitizing to estimation ranges (Figure 2H). Consequently, we propose that a single neural mechanism underlies both subitizing and estimation ranges. Nevertheless, a single neural mechanism may still have distinct perceptual consequences in different numerosity ranges due to the logarithmic nature of numerosity tuning functions. First, within each numerosity map, a higher proportion of neurons prefer low numerosities, and thus, more cortical area (Cai, Hofstetter, van Dijk, et al., 2021; Harvey et al., 2013; Harvey & Dumoulin, 2017a) is devoted to lower than to higher numerosities (Figure 2H). Second, since tuning width increases with preferred numerosity (Cai, Hofstetter, van Dijk, et al., 2021; Harvey et al., 2013; Harvey & Dumoulin, 2017a; Nieder & Miller, 2003; Piazza et al., 2004) (Figure 2I), the precision of the numerosity representation decreases with increasing numerosity. As a result, the discriminability between a presented numerosity and its neighbor (n vs $n + 1$) is very high, up to four items, but decreases dramatically beyond four items (Figure 2E). Above a certain discriminability, discrimination performance reaches a ceiling, becoming error-free (Figure 2D,F). Based on these results, we suggest that differences in neural tuning properties, such as tuning width, proportion of neurons with a preference for low versus high numerosity, and cortical area underlie distinct behavioral performances when judging low and high numerosities. This is well established in vision and other sensory systems, where perceptual differences are related to a similar change in number of neurons and neural tuning widths (Wandell et al., 2007; Wandell & Winawer, 2015). For example, central vision has a higher resolution and uniquely supports tasks like reading, which is supported by both narrower tuning widths (receptive fields) and more neurons devoted to processing central vision.

Thus, we propose that differences in tuning properties and proportion of neurons can explain the different behavioral phenomena such as Weber's law, subitizing, and estimation. Extending the notion of neural tuning underlying behavioral phenomena, several reports indicate that numerical education and numerosity perception interact (Butterworth, 2018). Therefore, we speculate that numerosity tuning may be influenced by education, and that neural tuning may undergo further refinement during developmental stages.

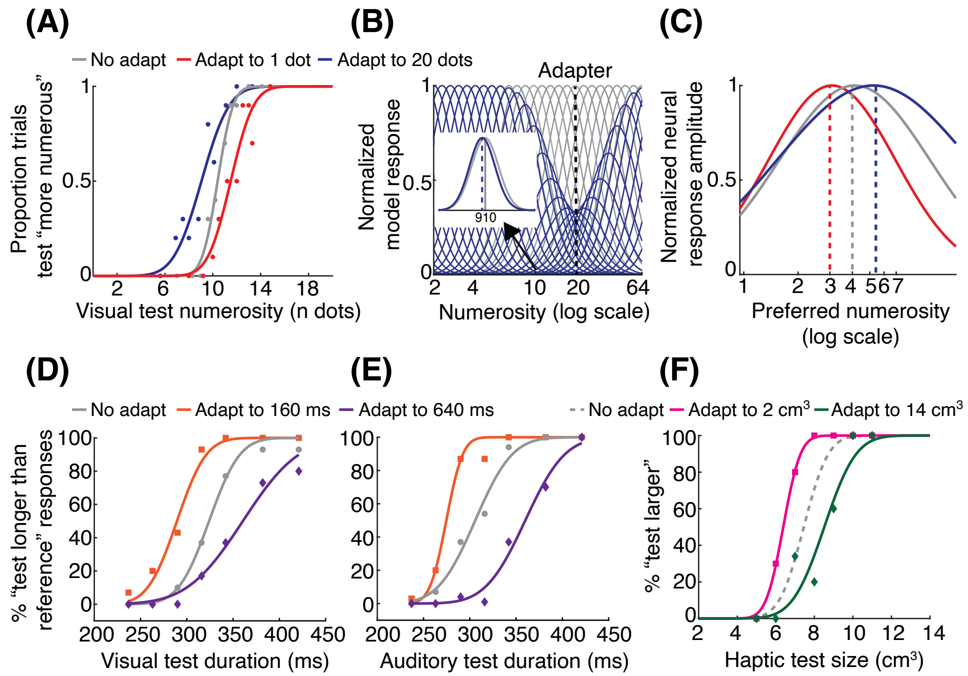


Figure 3. *Adaptation aftereffects in different quantities and sensory modalities*. (A) Adaptation to high (20) numerosity leads to underestimation of a subsequently presented low numerosity (reference stimulus), whereas adaptation to low (1) numerosity leads to an overestimation (data from: Tsouli et al., 2021). (B) These perceptual shifts can be explained by numerosity tuning, where repeated stimulation with a specific adapter stimulus suppresses the responses of neurons depending on the amplitude of their response to that stimulus. The population response to stimuli near the adapter will be biased away from the adapter, accounting for a repulsive perceptual shift. (C) Neural numerosity tuning within the subitizing range is altered by numerosity adaptation, with preferred numerosities being predominantly biased towards the numerosity of the adapter (data from: Tsouli et al., 2021). Similar adaptation aftereffects have been found in (D) visual and (E) auditory duration perception, where adaptation to a long (640 ms) versus short (160 ms) duration leads to an under- versus overestimation of a test stimulus's duration (drawn after: Heron, Aaen-Stockdale, et al., 2012). (F) Similarly, adaptation to a large (14 cm3) versus small (2 cm3) haptic object leads to repulsive changes in the perceived size of a test stimulus (drawn after: Kappers & Bergmann Tiest, 2014). Note that all psychometric curves presented in (A) and (D–F) show the same repulsive shift but differences in the direction of the curves (leftward versus rightward) are due to methodological differences [i.e., adaptation effect measured on the reference (A) or test stimulus (D–F)]. Thus, adaptation aftereffects are also present in different quantity dimensions and sensory modalities, indicating similar mechanisms.

Neural numerosity tuning can also account for the perceptual aftereffects produced by numerosity adaptation as measured using psychophysics. Psychophysical adaptation entails the repeated presentation of a particular adapter stimulus, which makes subsequently presented stimuli appear more different from the adapter than they are (Clifford et al., 2007; Kohn, 2007). Numerosity perception is highly susceptible to adaptation: adapting to a low numerosity leads to an overestimation of a numerosity subsequently presented, whereas adapting to a high numerosity leads to an underestimation (Burr et al., 2011, 2017; Burr & Ross, 2008; Tsouli, Dumoulin, et al., 2019; Tsouli et al., 2021) (Figure 3A).

A classic framework on the neural basis of adaptation after-effects views perception as the sum of responding neurons' preferred stimulus states, weighted by those neurons' response amplitude levels (Braddick et al., 1978; Clifford et al., 2000; Desimone, 1996; Heron, Aaen-Stockdale, et al., 2012). Repeated stimulation with a specific adapter stimulus leads to suppression of neurons' responses depending on how strongly they respond to that stimulus (Dragoi et al., 2000; Movshon & Lennie, 1979). Using this framework, numerosity adaptation can be modeled as the summed responses of a population of neurons with logarithmic Gaussian tuning functions, which display maximum response suppression at the adapter numerosity (numerosity of 20; Figure 3B). After adaptation, the population response to a presented numerosity will have less contribution from the units with a preferred numerosity near the adapter numerosity, biasing the population response away from the adapter (Figure 3B inset). This model is appealing since the neural population response follows the same bias as perception.

Using a numerosity adaptation paradigm combined with fMRI, we recently showed that neural numerosity tuning within a network of topographic numerosity maps was systematically altered by adaptation (Tsouli et al., 2021). Specifically, neural numerosity preferences were overall attracted to the adapter's numerosity (Figure 3C), with the extent of attraction increasing when the (unadapted) preferred numerosities were numerically further from the adapter's numerosity. When testing our fMRI adaptation paradigm psychophysically, we found repulsive perceptual aftereffects (Figure 3A), in agreement with other behavioral studies on numerosity adaptation.

The significance of our findings on neural numerosity adaptation is twofold. First, they underscore the relationship between neural tuning and perception, in particular since both are affected by adaptation. However, the direction of change in neural numerosity tuning does not match the predictions of the simple response–suppression models (Figure 3B), yet is consistent with our previous findings on changes in neural tuning and perception in the field of attention (Klein et al., 2014, 2016). Second, our results highlight that neural populations whose numerosity preferences fall within the subitizing range are also affected by adaptation (Figure 3C). Typically, perception of the subitizing range is immune to adaptation except under conditions of high attentional load (Burr et al., 2011). Hence, neural adaptation may seem inconsistent with the general absence of perceptual adaptation in the subitizing range. However, this difference can be explained by the properties of neural tuning. A small change in the response function of a population of neurons with a preference for a high numerosity can easily change its preferred numerosity by one or more (Figure 2B), so a different numerosity is perceived. We speculate that the same small change in the response function of a population of neurons with a preference for a very low numerosity may be insufficient to change its preferred numerosity by one (Figure 2B), so the perceived numerosity remains unchanged after adaptation. In other words, neural adaptation is likely too small to change the perceptual readout, since the perceptual readout is discrete. In summary, neural tuning unifies perceptual and neural effects of numerosity adaptation and further illustrates that subitizing and estimation perceptual ranges may be processed by a single neural mechanism.

Neural tuning underlies perception of other quantities and sensory modalities

Here, we consider other quantities and sensory modalities beyond visual numerosity. Like visual numerosity, we propose that neural tuning underlies the perception of other quantities and sensory modalities. We focus on perception of numerosity, object size, and timing in visual, auditory, and haptic modalities, whereas these mechanisms may well be absent in taste and smell.

Above, we explained how neural tuning may underlie adaptation of visual numerosity. Perceptual after-effects produced by adaptation also extend to other quantities, such as visual duration (Heron, Aaen-Stockdale, et al., 2012) (Figure 3D) and visual object size (Anobile, Burr, et al., 2018; Blakemore & Sutton, 1969; Pooresmaeili et al., 2013) and other sensory modalities, such as auditory numerosity (Arrighi et al., 2014) and auditory duration (Becker & Rasmussen, 2007; Heron, Aaen-Stockdale, et al., 2012) (Figure 3E). In the haptic modality, there is evidence for adaptation after-effects for tactile numerosity (Togoli et al., 2021), motor movement rate (Anobile et al., 2021), tactile duration (Li et al., 2019), and haptic object size (Kappers & Bergmann Tiest, 2014) (Figure 3F). Similar to visual numerosity (Figure 3A–C), we propose that changes in the responses of neurons with different tuning functions mediate these changes in perception.

Indeed, neural tuning is not restricted to visual numerosity but is also present in different quantities and sensory modalities. Single-cell recordings have shown neurons tuned to visual event duration (Duysens et al., 1996; Jazayeri & Shadlen, 2015; Leon & Shadlen, 2003), visual line-length (a measure of object size) (Eiselt & Nieder, 2016; Tudusciuc & Nieder, 2007, 2009), auditory temporal numerosity (Nieder, 2012; Thompson et al., 1970), and auditory duration (He et al., 1997). Although there is evidence for neural tuning to the number of self-produced actions (Sawamura et al., 2002) and for motor event timing (Merchant et al., 2013; Mita et al., 2009), no study has examined neural tuning to haptic numerosity (e.g., number of hand-held objects) or tactile duration using single-cell recordings. There is some electrophysiological evidence for neural tuning to haptic object size in nonhuman primates, where neurons respond preferentially to specific sizes of grasped objects (Gardner et al., 2007; Murata et al., 2000).

Human fMRI has contributed evidence of neural populations tuned to visual duration (Harvey et al., 2020; Hayashi et al., 2015; Protopapa et al., 2019), visual object size (Harvey et al., 2015), as well as visual line proportions (i.e., ratio of the length of two lines) (Jacob & Nieder, 2009). No fMRI study to date has examined neural tuning to auditory numerosity (e.g., number of tones) or auditory duration. There is evidence for neural tuning to haptic numerosity (Hofstetter et al., 2021; Hofstetter & Dumoulin, 2021), but neuroimaging evidence for neural tuning to haptic duration and haptic object size is lacking. Last, tuned responses to visual numerosity (Cai, Hofstetter, van Dijk, et al., 2021; Harvey et al., 2013; Harvey & Dumoulin, 2017a), visual event duration (Harvey et al., 2020; Protopapa et al., 2019), visual object size (Harvey et al., 2015), and haptic numerosity (Hofstetter et al., 2021; Hofstetter & Dumoulin, 2021) have been investigated using pRF modeling, and in these cases, the quantity-tuned populations have shown topographic organization.

Collectively, these results strongly suggest that neural tuning is a general property of neural quantity processing and consequently may underlie quantity perception in general. Therefore, and although the evidence is not complete for all different quantities and modalities, especially in the haptic domain, we hypothesize that neural tuning, arranged in topographic maps, may be found for many quantities and modalities.

Known properties of neural tuning appear to account for Weber's law in other quantities. For example, tuning curves in early visual timing maps become increasingly wider with increasing preferred duration (Harvey et al., 2020). Similarly, neurons tuned to visual line length show wider response functions for longer preferred lengths, and their population responses become less able to discriminate between longer lines (Tudusciuc & Nieder, 2007). In line with this observation, Weber's law appears to hold not only for visual numerosity perception but also perception of visual duration (Merchant et al., 2008; Wearden & Bray, 2001), visual length (Droit-Volet et al., 2008; Tudusciuc & Nieder, 2010), auditory numerosity (Hauser et al., 2003; Tokita & Ishiguchi, 2016), auditory duration (Brannon et al., 2008; Merchant et al., 2008; Murai & Yotsumoto, 2016, 2018; Wearden & Bray, 2001), tactile numerosity (Tokita & Ishiguchi, 2016), tactile duration (Azari et al., 2020; van Erp & Werkhoven, 2004), haptic size (Smeets & Brenner, 2008), and motor timing performance (Merchant et al., 2013). We therefore propose that properties consistent with Weber's law may be found in the neural tuning for many quantities and modalities.

However, systematic deviations from Weber's law have also been demonstrated (Burr et al., 2013; Grondin, 2014; Lewis & Miall, 2009; Wearden & Lejeune, 2008). We suggest that in the cases where quantity perception does not conform to Weber's law, the tuning profile of quantity-selective neural populations will reflect these perceptual effects. For example, perception of timing and object size are attracted to the middle of the presented range (Jazayeri & Shadlen, 2010; Kristensen et al., 2021); that is, the central tendency effect (Hollingworth, 1910). These bias effects may be accounted for by properties of neural tuning. Visual object size preferences are flexible with the range of presented object sizes (Kristensen et al., 2021), while visual timing tuning is finest in the middle of the presented range (Harvey et al., 2020). Therefore, although not all quantity perception follows Weber's law, systematic deviations from Weber's law may still reflect other properties of quantity-tuned neural populations.

Another deviation from Weber's law is subitizing. Separate subitizing and estimation mechanisms are also present in auditory (Camos & Tillmann, 2008) and haptic numerosity judgements (Cohen & Henik, 2015; Gallace et al., 2008; Hofstetter et al., 2021; Plaisier et al., 2009) but not observed in other quantities. This can be explained by the discrete nature of numerosity compared to the continuous nature of other quantities.

Based on the above, we propose that tuned responses and topographic organization are common across quantity processing, but evidence of these properties is not complete for all quantities and modalities. Specifically, we hypothesize the presence of topographic maps for numerosity and timing in the auditory modality, and timing and object size in the haptic modality, and suggest that these maps may overlap with maps for other quantities. Additionally, the precise role of the distinct topographic maps in quantity perception is currently unclear. Moreover, a causal link between quantity tuning and quantity perception is highly plausible but remains to be established. We hypothesize that stimulation or manipulation of specific quantity-tuned neurons should alter quantity perception.

Neural tuning underlies interactions between different quantities

Given the evidence for the existence of neural populations tuned to different quantities and sensory modalities, and the role of neural tuning in quantity perception, we suggest that neural tuning is an invaluable mechanism for disentangling potential interactions between different quantities. A number of theories (Bonn & Cantlon, 2012; Church & Broadbent, 1990; Gallistel & Gelman, 2000; Walsh, 2003) postulate that different quantities might share computational and/or neural mechanisms. These theories are supported by neuroimaging findings showing overlapping brain activations during different quantity tasks (Cantlon et al., 2009; Cohen Kadosh et al., 2008; Sokolowski et al., 2017) and perceptual interactions between quantity dimensions. However, overlapping brain activations do not necessarily imply a common neural code for different quantities, and recent behavioral studies examining the interaction of different quantities paint a more complex picture (Hamamouche & Cordes, 2019; Tsouli, Dumoulin, et al., 2019; Tsouli, van der Smagt, et al., 2019). Furthermore, evidence from animal electrophysiology and human fMRI are not entirely consistent with the idea of a common neural mechanism for different quantities. Single-cell recordings reveal that neurons responding to different quantities such as numerosity, size (line length), spatial frequency, duration and distance are anatomically intermingled, but most neurons encode only one type of quantity (Eiselt & Nieder, 2016; Marcos et al., 2017; Tudusciuc & Nieder, 2007, 2009). A minority of neurons are tuned to multiple quantities, but preferences for these different quantities are not correlated so their tuning functions appear independent. Nevertheless, small proportions of neurons are tuned to numerical quantity in the visual and auditory modality (Nieder, 2012), and visual numerosity and visual line length (Tudusciuc & Nieder, 2007); therefore, we cannot exclude the possibility that a subpopulation of neurons might serve as abstract quantity detectors. Hence, further examining the tuning of single neurons to multiple quantities and their link to perception will be pivotal in elucidating whether related tuned responses are sufficient for generalized quantity processing.

In humans, we have revealed neural populations tuned to different quantities in nearby anatomical locations (Figure 4A), forming topographic maps of visual numerosity (Cai, Hofstetter, van Dijk, et al., 2021; Harvey et al., 2013; Harvey & Dumoulin, 2017a), haptic numerosity (Hofstetter et al., 2021), visual object size (Harvey et al., 2015), and visual timing (Harvey et al., 2020) (Figure 4B–E). Moreover, these neural populations are not restricted to the cortex but also found in subcortical nuclei (Hofstetter & Dumoulin, 2021). What do these tuned neural responses and topographic maps tell us about potential interactions between different quantities? When combining our individual findings on neural tuning to different quantities, we observe that neural responses to visual and haptic numerosity, object size and timing spatially overlap to a large extent. However, at a finer scale each quantity is processed by distinct topographic maps. For example, in the case of visual numerosity and haptic numerosity (Hofstetter et al., 2021) or visual object size (Harvey et al., 2015), we find neural selectivity in similar cortical regions but distinct maps, indicating that the responses of the underlying neural populations remain primarily quantity- and modality-specific (Figure 4B–D).

Based on all the above, we propose that observed commonalities in neural and behavioral representations between quantities are not accounted for by a common neural representational code across quantities, but by the interaction of spatially intermingled neural populations which are independently tuned to different quantities and modalities. The question then arises how these independently tuned neurons are organized and interact within the topographic maps.

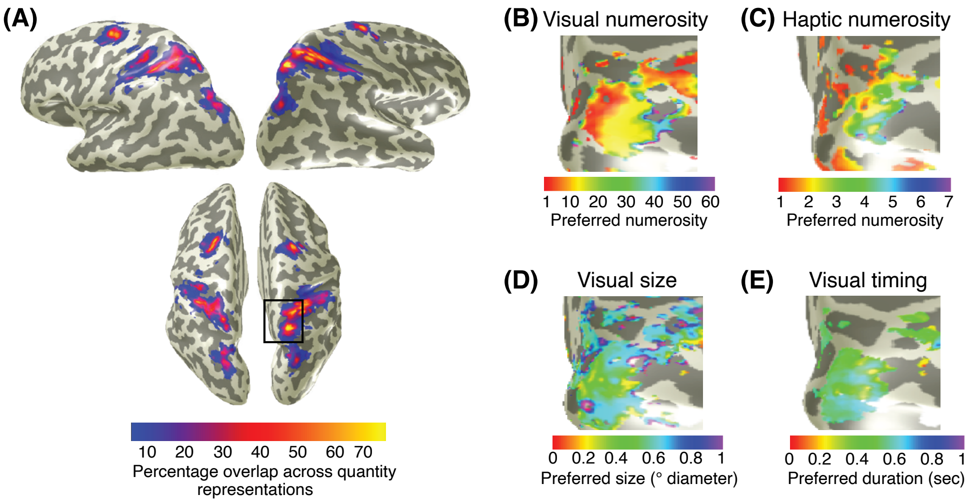


Figure 4. *Topographic quantity maps*. (A) The network of topographic maps of each quantity overlaps in the parietal and frontal lobes. The color map indicates the percentage of overlap between participants across four different quantity dimensions [individual participant maps of each quantity were transformed onto the N27 (Talairach) template's cortical surface]. The square highlights the region of the superior parietal lobule in which we show the four topographic maps in panels B–E for one participant. Selective responses to each quantity are organized into topographic maps, that is, regions where the preferred quantity changes gradually across the cortical surface. The topographic maps of (B) visual numerosity (data from: Cai, Hofstetter, van Dijk, et al., 2021), (C) haptic numerosity (data from: Hofstetter et al., 2021), (D) object size (data from: Harvey et al., 2015) and (E) timing (data from: Harvey et al., 2020) overlap, but are distinct.

In primary cortices, these independently tuned neurons are organized in columnar and laminar structures within topographic maps. Recently, we suggested that laminar organization of numerosity maps follow that of primary cortices (van Dijk et al., 2021). We speculate that a similar organization exists in quantity maps and may reveal the basis of their interaction (Dumoulin et al., 2018).

Concluding remarks

The ability to perceive quantity information, such as numerosity, timing, and object size, is fundamental to cognition. In agreement with previous authors (Nieder, 2020a; Nieder & Dehaene, 2009), we argue that neural tuning links perception to the brain's responses, serves as the neural basis underlying quantity processing, and can explain many behavioral effects in quantity perception, such as the numerical size and distance effects. In addition, recent neuroimaging studies show how neural tuning properties can also explain and unify the subitizing and estimation ranges, adaptation effects and interactions between quantities and sensory modalities. By endorsing the value of neural tuning in explaining the cognitive representations of quantities, new research avenues open up, ranging from neural quantity tuning in different developmental stages to the further exploration of the link between neural tuning, topographic quantity maps and quantity perception (see Outstanding questions).

Outstanding questions

Tuning has been found for many quantities, in some cases with topographic organization by preferred quantity. Do these principles apply to other quantities? We propose that tuned responses and topographic organization are common across quantity processing, but evidence of these properties is not complete for all quantities and modalities.

There are extensive networks of topographic maps representing many quantities. What is the role in quantity perception for the distinct maps within the network? In sensory systems, different topographic maps are often associated with different functions. Several maps have been found for each quantity, yet the links between different cognitive functions and different maps are unclear.

The link between neural tuning and perception is correlational – can we establish a causal link? We advocate for the role of neural tuning in perception, but this is not the only theory. Given our proposal, we hypothesize that stimulation or manipulation of specific quantity-tuned neurons should alter quantity perception.

How does neural tuning for quantities develop and is it altered as new skills are learned? Many behavioral developmental studies relate quantity perception to cognition in children. Yet, most neural studies, and in particular those studying quantity tuning, are in healthy adults.

How do differential attractive and repulsive changes in neural quantity tuning due to adaptation relate to perceptual changes? Adaptation produces both repulsive and attractive changes in neural tuning. Attraction of quantity preferences is not readily explained by simple response–suppression models. The perceptual effects of these changes in tuning are still poorly understood.

How is quantity tuning organized on the mesoscopic scale of the brain? In the visual cortex, at the mesoscopic scale, multiple features are organized in laminae and columns within the same topographic map. We speculate that neurons responding to different quantities and modalities may be held together in similar spatially distinct fine-scale neural structures.

Chapter 6

General Discussion

In this thesis, we examined the neural mechanisms subserving the perception of numerosity and other quantities. We used neuroimaging and psychophysics and further integrated different sources of evidence which allowed us to show how tuned neural mechanisms may underly the perception of different quantities.

Adaptation changes neural numerosity tuning

In **Chapter 2**, we examined whether and how neural numerosity selectivity changes during numerosity adaptation. To study this, we used ultra-high field (7 Tesla) fMRI, custom-build pRF neural models of numerosity encoding, and a visual adaptation paradigm. We showed that neural numerosity selectivity within the network of topographic numerosity maps was altered by adaptation. Specifically, neural numerosity preferences were predominantly attracted to the numerosity of the adapter, with the extent of attraction increasing when the unadapted preferred numerosities were numerically further from the numerosity of the adapter. The same pattern of this adaptation-induced change in neural tuning was observed in all numerosity maps despite their wide structural separation across the cortical surface. This reinforces the idea that these numerosity maps constitute a unified numerosity-encoding network which could underlie numerosity processing.

Moreover, we suggested that the attractive biases we found in neural numerosity tuning could predict repulsive perceptual aftereffects consistent with those measured psychophysically. Our proposal is based on findings showing similarly distinct changes in neural tuning and perception in the field of attention (Klein et al., 2014, 2016), as well as findings from electrophysiological studies on orientation (Jin et al., 2005) and motion direction tuning (Kohn & Movshon, 2004). Specifically, and in the case of motion direction tuning in area MT, adaptation at near-preferred directions ('flank' adaptation) was shown to shift tuning toward the adapted direction. Modeling the effect of adaptation in MT further showed that these attractive shifts in tuning can explain repulsion of perceived motion after adaptation when measured psychophysically (Kohn & Movshon, 2004).

More generally, the functional benefits of said changes in neural tuning after adaptation and their link to perception remain to be established. One hypothesis is that the functional consequence of adaptation is to enhance discriminability of stimuli which are more similar to the recently encountered mean, by re-centering tuning around prevailing stimulus conditions (Kohn, 2007, p. 3160; Krekelberg et al., 2006). However, robust evidence for such a relationship between changes in neural tuning and discriminability is currently lacking. Another compelling proposal is that adaptation-induced changes in neural tuning facilitate the detectability of novel stimuli by suppressing neural responses to recurrent stimuli and by enhancing neural responses to novel stimuli (Clifford et al., 2001; Dragoi et al., 2002; Kohn, 2007). It has also been suggested that adaptation increases coding efficiency through 'decorrelation' of neural population activity which results to fewer neurons being active and thus, allows metabolic savings (Barlow & Földiák, 1989; Kohn, 2007; Müller et al., 1999). In the case of numerosity, electrophysiological studies using an adaptation paradigm combined with perceptual measurements are needed to shed more light on the link between attractive versus repulsive changes in neural numerosity tuning and numerosity perception.

Adaptation to duration alters numerosity perception

In **Chapter 3**, we investigated the possible existence of neural substrates which are tuned to both numerosity and time, guided by theories postulating common neural mechanisms for these quantities (Bonn & Cantlon, 2012; Bueti & Walsh, 2009; Cantlon et al., 2009; Meck & Church, 1983; Walsh, 2003). We used adaptation and psychophysics which allowed us to infer the existence of tuned mechanisms implicated in numerosity and time perception. Previous studies have shown the existence of a repulsive numerosity aftereffect in the visual domain (Aagten-Murphy & Burr, 2016; Burr et al., 2017; Burr & Ross, 2008). Similarly, adaptation to duration has also been shown to yield repulsive perceptual aftereffects in perceived duration in the visual and auditory domain (Heron, Aaen-Stockdale, et al., 2012; Heron et al., 2013; Li et al., 2015; Shima et al., 2016). We used a cross-adaptation paradigm and reasoned that if numerosity and time perception rely on shared, tuned mechanisms, then adaptation to visual numerosity should affect visual duration discrimination, and adaptation to visual duration should affect visual numerosity discrimination. First, we replicated the numerosity and duration aftereffects and further showed that both numerosity and duration adapt even when using a rapid adaptation paradigm entailing brief adaptation periods and few trials. In addition, we found that adaptation to visual duration altered the perception of visual numerosity in a repulsive manner. However, adaptation to numerosity did not significantly affect duration perception. Hence, we suggested that although unbalanced, there is an interaction between the tuned mechanisms involved in numerosity and duration perception. One possible explanation we offered for this unbalanced interaction is that numerosity and duration tuning arise at different processing stages, leading to a differential influence of one over the other.

More generally, the adaptation paradigm we employed can be used to address pending questions about quantity processing in typical and atypical populations. For instance, an ongoing debate in numerosity research is the role of (non-symbolic) numerosity in developmental dyscalculia, and the potential role of other quantities such as duration and object size. Deficits in processing numerosity (Mazzocco et al., 2011; Piazza et al., 2010; Pinheiro-Chagas et al., 2014), duration, and size (De Visscher et al., 2018; Skagerlund

& Träff, 2014; Vicario et al., 2012) have been previously reported in individuals with dyscalculia. However, these findings have not gone undisputed (numerosity: Iuculano et al., 2008; Rousselle & Noël, 2007; duration: Cappelletti, Freeman, & Butterworth, 2011; object size: Castaldi et al., 2018). We suggest that using a (cross-)adaptation paradigm to different quantities can be a valuable tool to further elucidate the neural and perceptual underpinnings of numerical, temporal, and spatial quantities and their possible involvement in individuals with intact or impaired mathematical abilities.

Distinct duration processes affect numerosity perception

In **Chapter 4**, we described two follow-up experiments we conducted to elucidate the nature of the interaction between numerosity and duration shown in Chapter 3. In both experiments, we manipulated different duration parameters and specifically the onset/offset duration of the adapter, the total presentation duration of the adapter and the total duration of the adaptation trial.

The first experiment tested the effect of adaptation to visual duration on visual numerosity discrimination. We reasoned that if the influence of duration on numerosity perception is due to the adaptation of duration channels tuned to the onset/offset duration of the adapter, then the adaptation conditions where the adapter's onset/offset duration was short (67 ms) versus long (600 ms) would drive the repulsive aftereffect on numerosity perception. However, if the effect of adaptation to duration is not driven by duration-tuned mechanisms but rather reflects the adaptation of numerosity-tuned mechanisms only, then a short (67 ms) versus long (1800 ms) total duration of the adaptation trial would underlie the repulsive aftereffect on numerosity perception. This would be in accordance with a common observation in adaptation research showing that longer adaptation periods result in stronger perceptual aftereffects (Dragoi et al., 2000; Hershenson, 1989; Magnussen & Johnsen, 1986). We found that that the effect of adaptation to duration on numerosity discrimination reflects the adaptation of duration-selective channels since the conditions where the onset/offset duration of the adapter was the same (67 ms) produced similar adaptation effects, and were overall different from the condition where the onset/offset duration was longest (600 ms).

The second experiment tested the combined effect of adaptation to duration and adaptation to numerosity on numerosity discrimination. We reasoned that if the effect of duration on numerosity perception is not a result of adapting duration-selective channels but a result of adapting numerosity-tuned channels for a longer time period, then the total duration of the adaptation trial would drive the numerosity aftereffect. We found that the duration condition with the longest total duration of the adaptation trial (1800 ms) produced the strongest perceptual aftereffects, even if the adapter's onset/offset duration was very short (67 ms). Hence, and when examining adaptation to numerosity, the influence of duration can be explained by the strength of adaptation of numerosity-selective channels only, without the involvement of duration-selective channels. Based on the distinct temporal influences we found in these two experiments, we speculated that the neural populations underlying the effect of *adaptation to duration* on numerosity perception are partially distinct from those underlying the effect of the *duration of adaptation* on numerosity perception.

Examining the processing stages of the numerosity and duration aftereffect

Given the unidirectional effect of adaptation to duration on numerosity perception we describe in Chapter 3, we speculated that duration tuning could arise at lower areas of the visual cortex compared to numerosity tuning. This implies the existence of a processing hierarchy where duration information processing precedes numerosity processing. Psychophysically, a method to infer the position of these aftereffects within the visual hierarchy is by using a monocular (same eye) versus dichoptic (different eyes) presentation paradigm. This method takes advantage of the functional architecture of the visual cortex. Specifically, the primary visual cortex (V1) is considered the earliest stage at which input from the two eyes converges onto binocular neurons (Horton et al., 1990; Hubel & Wiesel, 1962, 1968; Menon et al., 1997). Hence, and by examining the degree of interocular transfer of the numerosity and duration aftereffect, we can infer whether numerosity and duration selectivity arises within processing stages at or above those subserved by neural populations in V1. We designed an experiment where adapter and test stimuli were presented either monocularly or dichoptically using a two-mirror stereoscope, and aimed to test adaptation to numerosity, adaptation to duration, and cross-adaptation between the two quantities.

Given our previously reported unbalanced interaction between numerosity and duration, we predicted that the numerosity and duration aftereffect would display a different degree of interocular transfer, with the duration aftereffect showing a greater monocular component (i.e., occurring at earlier processing stages) compared to the numerosity aftereffect (see also Figure 1 for overview of our experimental design and predictions). Although we could not collect data for this experiment due to COVID-19-related restrictions, this psychophysical paradigm could shed more light on the processing stages underlying numerosity and duration perception and allow us to infer the position of the possibly shared tuned mechanisms underlying numerosity and duration perception within the visual hierarchy.

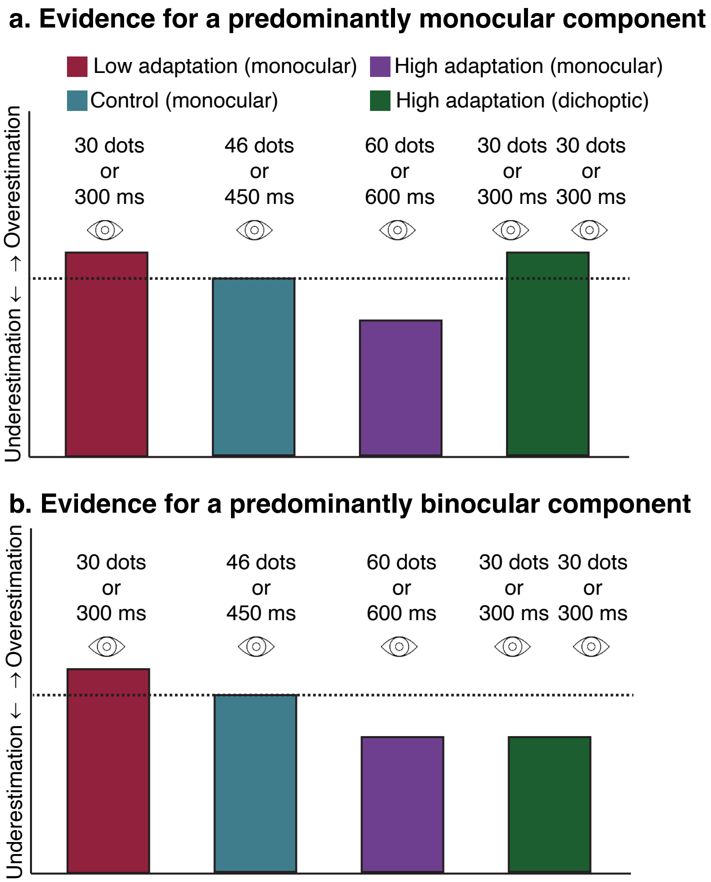


Figure 1. *Research design and predictions for examining the processing stages involved in the numerosity and duration aftereffects.* We designed an experiment where the numerosity or duration adapters were presented monocularly or dichoptically. (a) We predict that if the numerosity and duration aftereffects are driven by primarily monocular mechanisms and thus, show no interocular transfer, then the condition where a low numerosity or duration adapter is presented monocularly (red bar) will yield a similar adaptation effect (i.e., overestimation of the reference stimulus) to the condition where a high numerosity or duration adapter is presented dichoptically (green bar). (b) Conversely, if the numerosity and duration aftereffects are driven by primarily binocular mechanisms and thus, exhibit complete interocular transfer, then the conditions where a high adapter is presented monocularly (purple bar) or dichoptically will produce a similar adaptation effect (i.e., underestimation of the reference stimulus).

Neural tuning underlies quantity perception

The interaction between different quantities such as numerosity, time, and space has been studied extensively in recent decades (see review Hamamouche & Cordes, 2019), yet how the neural substrates encoding these quantities give rise to different behavioral phenomena remains elusive. In **Chapter 5**, we integrated recent electrophysiological, neuroimaging, and psychophysical evidence showing neural tuning for different quantities and sensory modalities, and proposed that neural quantity tuning is critical for quantity perception. Our proposal was guided by known links between brain and perception in primary sensory and motor cortices, where neural tuning and topographic mapping are thoroughly established. We illustrated how the properties of neurons tuned to numerical, temporal or spatial quantities appear to underlie seminal psychophysical laws and behavioral phenomena in numerosity, timing and size perception. We further proposed that spatially intermingled neural populations which are independently tuned to different quantities provide the neural basis for perceptual interactions between different quantities, without necessitating the existence of a common neural representational code across quantities as previously suggested (Bonn & Cantlon, 2012; Bueti & Walsh, 2009; Cantlon et al., 2009; Meck & Church, 1983; Walsh, 2003).

Conclusion

The findings of this thesis add to our understanding of the properties of neural numerosity selectivity and further show how numerosity-tuned mechanisms interact with duration-tuned mechanisms. Moreover, and based on evidence showing the existence of neural populations tuned to different quantities and in different sensory modalities, we propose that neural quantity tuning is fundamental for quantity perception. We further suggest that neural tuning is a crucial mechanism for understanding the neural underpinnings of perceptual interactions between different types of quantities. Ultimately, the implications of the topics covered in this thesis provide an answer as to why cognitive scientists should care about neurons, and provide the framework for new research avenues. So stay tuned for more (or less).

Appendix

References

References

Aagten-Murphy, D., & Burr, D. (2016). Adaptation to numerosity requires only brief exposures, and is determined by number of events, not exposure duration. *Journal of Vision*, *16*(10), 22. https://doi.org/10.1167/16.10.22

Abdullaev, Y. G., & Melnichuk, K. V. (1996). Counting and arithmetic functions of neurons in the human parietal cortex. *NeuroImage*, *3*(3), S216.

Agrillo, C., & Bisazza, A. (2017). Understanding the origin of number sense: A review of fish studies. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *373*(1740), 20160511. PubMed. https://doi.org/10.1098/rstb.2016.0511

Agrillo, C., Piffer, L., & Adriano, A. (2013). Individual differences in non-symbolic numerical abilities predict mathematical achievements but contradict ATOM. *Behavioral and Brain Functions*, *9*(1), 26. https://doi.org/10.1186/1744-9081-9-26

Agrillo, C., Ranpura, A., & Butterworth, B. (2010). Time and numerosity estimation are independent: Behavioral evidence for two different systems using a conflict paradigm. *Cognitive Neuroscience*, *1*(2), 96–101. https://doi.org/10.1080/17588921003632537

Alards-Tomalin, D., Walker, A. C., Kravetz, A., & Leboe-McGowan, L. C. (2016). Numerical Context and Time Perception: Contrast Effects and the Perceived Duration of Numbers. *Perception*, *45*(1–2), 222–245. https://doi.org/10.1177/0301006615594905

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology*, *52*(6), 1106–1130. https://doi.org/10.1152/jn.1984.52.6.1106

Allik, J., & Tuulmets, T. (1991). Occupancy model of perceived numerosity. *Perception & Psychophysics*, *49*(4), 303–314. https://doi.org/10.3758/BF03205986

Andersson, J. L. R., Skare, S., & Ashburner, J. (2003). How to correct susceptibility distortions in spin-echo echo-planar images: Application to diffusion tensor imaging. *NeuroImage*, *20*(2), 870–888. https://doi.org/10.1016/S1053-8119(03)00336-7

Anobile, G., Arrighi, R., Castaldi, E., & Burr, D. C. (2021). A Sensorimotor Numerosity System. *Trends in Cognitive Sciences*, *25*(1), 24–36. https://doi.org/10.1016/j.tics.2020.10.009

Anobile, G., Burr, D., Iaia, M., Marinelli, C. V., Angelelli, P., & Turi, M. (2018). Independent adaptation mechanisms for numerosity and size perception provide evidence against a common sense of magnitude. *Scientific Reports*, *8*(1), 13571. https://doi.org/10.1038/s41598-018-31893-6

Anobile, G., Cicchini, G. M., & Burr, D. (2014). Separate Mechanisms for Perception of Numerosity and Density. *Psychological Science*, *25*(1), 265–270. https://doi.org/10.1177/0956797613501520

Anobile, G., Cicchini, G. M., & Burr, D. (2016). Number As a Primary Perceptual Attribute: A Review. *Perception*, *45*(1–2), 5–31. https://doi.org/10.1177/0301006615602599

Anobile, G., Cicchini, G. M., Gasperini, F., & Burr, D. C. (2018). Typical numerosity adaptation despite selectively impaired number acuity in dyscalculia. *Neuropsychologia*, *120*, 43–49. https://doi.org/10.1016/j.neuropsychologia.2018.10.006

Anobile, G., Turi, M., Cicchini, G. M., & Burr, D. C. (2012). The effects of cross-sensory attentional demand on subitizing and on mapping number onto space. *Vision Research*, *74*, 102–109. https://doi.org/10.1016/j.visres.2012.06.005

Anobile, G., Turi, M., Cicchini, G. M., & Burr, D. C. (2015). Mechanisms for perception of numerosity or texture-density are governed by crowding-like effects. *Journal of Vision*, *15*(5), 4. https://doi.org/10.1167/15.5.4

Ansari, D., Dhital, B., & Siong, S. C. (2006). Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes. *Brain Research*, *1067*(1), 181–188. https://doi.org/10.1016/j.brainres.2005.10.083

Arrighi, R., Togoli, I., & Burr, D. C. (2014). A generalized sense of number. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), 20141791. https://doi.org/10.1098/rspb.2014.1791

Atkinson, J., Campbell, F. W., & Francis, M. R. (1976). The Magic Number 4 ± 0: A New Look at Visual Numerosity Judgements. *Perception*, *5*(3), 327–334. https://doi.org/10.1068/p050327

Aubie, B., Sayegh, R., & Faure, P. A. (2012). Duration Tuning across Vertebrates. *Journal of Neuroscience*, *32*(18), 6373–6390. https://doi.org/10.1523/JNEUROSCI.5624-11.2012

Azari, L., Mioni, G., Rousseau, R., & Grondin, S. (2020). An analysis of the processing of intramodal and intermodal time intervals. *Attention, Perception, & Psychophysics*, *82*(3), 1473–1487. https://doi.org/10.3758/s13414-019-01900-7

Balakrishnanl, J. D., & Ashby, F. G. (1992). Subitizing: Magical numbers or mere superstition? *Psychological Research*, *54*(2), 80–90. https://doi.org/10.1007/BF00937136

Barlow, H., & Földiák, P. (1989). Adaptation and Decorrelation in the Cortex. In *The Computing Neuron* (pp. 54–72). Addison-Wesley Longman Publishing Co., Inc.

Barth, H., La Mont, K., Lipton, J., & Spelke, E. S. (2005). Abstract number and arithmetic in preschool children. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(39), 14116. https://doi.org/10.1073/pnas.0505512102

Becker, M. W., & Rasmussen, I. P. (2007). The rhythm aftereffect: Support for time sensitive neurons with broad overlapping tuning curves. *Brain and Cognition*, *64*(3), 274–281. https://doi.org/10.1016/j.bandc.2007.03.009

Blake, R., & He, S. (2005). Adaptation as a Tool for Probing the Neural Correlates of Visual Awareness: Progress and Precautions. In *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision*. Scopus. https://doi.org/10.1093/acprof:oso/9780198529699.003.0011

Blakemore, C., & Cooper, G. F. (1970). Development of the Brain depends on the Visual Environment. *Nature*, *228*(5270), 477–478. https://doi.org/10.1038/228477a0

Blakemore, C., Nachmias, J., & Sutton, P. (1970). The perceived spatial frequency shift: Evidence for frequency-selective neurones in the human brain. *The Journal of Physiology*, *210*(3), 727–750. https://doi.org/10.1113/jphysiol.1970.sp009238

Blakemore, C., & Sutton, P. (1969). Size Adaptation: A New Aftereffect. *Science*, *166*(3902), 245. https://doi.org/10.1126/science.166.3902.245

Bonn, C. D., & Cantlon, J. F. (2012). The origins and structure of quantitative concepts. *Cognitive Neuropsychology*, *29*(1–2), 149–173. https://doi.org/10.1080/02643294.2012.707122

Braddick, O., Campbell, F. W., & Atkinson, J. (1978). Channels in vision: Basic aspects. *Handbook of Sensory Physiology*, *8*, 3–38. Scopus.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Brand, A., Urban, R., & Grothe, B. (2000). Duration Tuning in the Mouse Auditory Midbrain. *Journal of Neurophysiology*, *84*(4), 1790–1799. https://doi.org/10.1152/jn.2000.84.4.1790

Brannon, E. M., Libertus, M. E., Meck, W. H., & Woldorff, M. G. (2008). Electrophysiological Measures of Time Processing in Infant and Adult Brains: Weber's Law Holds. *Journal of Cognitive Neuroscience*, *20*(2), 193–203. https://doi.org/10.1162/jocn.2008.20016

Brannon, E. M., Lutz, D., & Cordes, S. (2006). The development of area discrimination and its implications for number representation in infancy. *Developmental Science*, *9*(6), F59–F64. https://doi.org/10.1111/j.1467-7687.2006.00530.x

Brannon, E. M., & Terrace, H. S. (2000). Representation of the numerosities 1–9 by rhesus macaques (Macaca mulatta). *Journal of Experimental Psychology: Animal Behavior Processes*, *26*(1), 31–49. https://doi.org/10.1037/0097-7403.26.1.31

Brindley, G. S., & Lewin, W. S. (1968). The sensations produced by electrical stimulation of the visual cortex. *The Journal of Physiology*, *196*(2), 479–493. PubMed. https://doi.org/10.1113/jphysiol.1968.sp008519

Bruno, A., & Cicchini, G. M. (2016). Multiple channels of visual time perception. *Current Opinion in Behavioral Sciences*, *8*, 131–139. https://doi.org/10.1016/j.cobeha.2016.02.028

Buckley, P. B., & Gillman, C. B. (1974). Comparisons of digits and dot patterns. *Journal of Experimental Psychology*, *103*(6), 1131–1136. https://doi.org/10.1037/h0037361

Bueti, D. (2011). The Sensory Representation of Time. *Frontiers in Integrative Neuroscience*, *5*, 34. https://doi.org/10.3389/fnint.2011.00034

Bueti, D., & Walsh, V. (2009). The parietal cortex and the representation of time, space, number and other magnitudes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1525), 1831–1840. https://doi.org/10.1098/rstb.2009.0028

Bulthé, J., De Smedt, B., & Op de Beeck, H. P. (2014). Format-dependent representations of symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern analyses. *NeuroImage*, *87*, 311–322. https://doi.org/10.1016/j.neuroimage.2013.10.049

Buonomano, D. V., & Laje, R. (2010). Population clocks: Motor timing with neural dynamics. *Trends in Cognitive Sciences*, *14*(12), 520–527. https://doi.org/10.1016/j.tics.2010.09.002

Buonomano, & Karmarkar. (2002). How do we tell time? *Neuroscientist, The*, *8*(1), 42–51. /z-wcorg/.

Burr, D., Anobile, G., & Arrighi, R. (2017). Psychophysical evidence for the number sense. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1740), 20170045. https://doi.org/10.1098/rstb.2017.0045

Burr, D., Anobile, G., & Turi, M. (2011). Adaptation Affects Both High and Low (Subitized) Numbers Under Conditions of High Attentional Load. *Seeing and Perceiving*, *24*(2), 141–150. https://doi.org/10.1163/187847511X570097

Burr, D. C., Turi, M., & Anobile, G. (2010). Subitizing but not estimation of numerosity requires attentional resources. *Journal of Vision*, *10*(6), 20–20. https://doi.org/10.1167/10.6.20

Burr, D., Rocca, E. D., & Morrone, M. C. (2013). Contextual effects in interval-duration judgements in vision, audition and touch. *Experimental Brain Research*, *230*(1), 87–98. https://doi.org/10.1007/s00221-013-3632-z

Burr, D., & Ross, J. (2008). A Visual Sense of Number. *Current Biology*, *18*(6), 425–428. https://doi.org/10.1016/j.cub.2008.02.052

Burr, D., Tozzi, A., & Morrone, M. C. (2007). Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nature Neuroscience*, *10*(4), 423–425. https://doi.org/10.1038/nn1874

Butterworth, B. (2018). The implications for education of an innate numerosity-processing mechanism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1740), 20170118. https://doi.org/10.1098/rstb.2017.0118

Cai, Y., Hofstetter, S., van der Zwaag, W., Zuiderbaan, W., & Dumoulin, S. O. (2021). Individualized cognitive neuroscience needs 7T: Comparing numerosity maps at 3T and 7T MRI. *NeuroImage*, *237*, 118184. https://doi.org/10.1016/j.neuroimage.2021.118184

Cai, Y., Hofstetter, S., van Dijk, J., Zuiderbaan, W., van der Zwaag, W., Harvey, B. M., & Dumoulin, S. O. (2021). Topographic numerosity maps cover subitizing and estimation ranges. *Nature Communications*, *12*(1), 3374. https://doi.org/10.1038/s41467-021-23785-7

Cai, Z. G., & Connell, L. (2015). Space-time interdependence: Evidence against asymmetric mapping between time and space. *Cognition*, *136*, 268–281. https://doi.org/10.1016/j.cognition.2014.11.039

Camos, V., & Tillmann, B. (2008). Discontinuity in the enumeration of sequentially presented auditory and visual stimuli. *Cognition*, *107*(3), 1135–1143. https://doi.org/10.1016/j.cognition.2007.11.002

Cantlon, J. F., & Brannon, E. M. (2006). Shared System for Ordering Small and Large Numbers in Monkeys and Humans. *Psychological Science*, *17*(5), 401–406. https://doi.org/10.1111/j.1467-9280.2006.01719.x

Cantlon, J. F., & Brannon, E. M. (2007). Basic Math in Monkeys and College Students. *PLOS Biology*, *5*(12), e328. https://doi.org/10.1371/journal.pbio.0050328

Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional Imaging of Numerical Processing in Adults and 4-y-Old Children. *PLoS Biology*, *4*(5), e125. https://doi.org/10.1371/journal.pbio.0040125

Cantlon, J. F., Platt, M. L., & Brannon, E. M. (2009). Beyond the number domain. *Trends in Cognitive Sciences*, *13*(2), 83–91. https://doi.org/10.1016/j.tics.2008.11.007

Cappelletti, M., Chamberlain, R., Freeman, E. D., Kanai, R., Butterworth, B., Price, C. J., & Rees, G. (2014). Commonalities for Numerical and Continuous Quantity Skills at Temporo-parietal Junction. *Journal of Cognitive Neuroscience*, *26*(5), 986–999. https://doi.org/10.1162/jocn_a_00546

Cappelletti, M., Freeman, E. D., & Butterworth, B. L. (2011). Time Processing in Dyscalculia. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00364

Cappelletti, M., Freeman, E. D., & Cipolotti, L. (2009). Dissociations and interactions between time, numerosity and space processing. *Neuropsychologia*, *47*(13), 2732–2748. https://doi.org/10.1016/j.neuropsychologia.2009.05.024

Cappelletti, M., Freeman, E. D., & Cipolotti, L. (2011). Numbers and time doubly dissociate. *Neuropsychologia*, *49*(11), 3078–3092. https://doi.org/10.1016/j.neuropsychologia.2011.07.014

Carey, S. (2000). The Origin of Concepts. *Journal of Cognition and Development*, *1*(1), 37–41. https://doi.org/10.1207/S15327647JCD0101N_3

Castaldi, E., Aagten-Murphy, D., Tosetti, M., Burr, D., & Morrone, M. C. (2016). Effects of adaptation on numerosity decoding in the human brain. *NeuroImage*, *143*, 364–377. https://doi.org/10.1016/j.neuroimage.2016.09.020

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*, e45160. PubMed. https://doi.org/10.7554/eLife.45160

Castelli, F., Glaser, D. E., & Butterworth, B. (2006). Discrete and analogue quantity processing in the parietal lobe: A functional MRI study. *Proceedings of the National Academy of Sciences*, *103*(12), 4693–4698. https://doi.org/10.1073/pnas.0600444103

Cavdaroglu, S., & Knops, A. (2019). Evidence for a Posterior Parietal Cortex Contribution to Spatial but not Temporal Numerosity Perception. *Cerebral Cortex*, *29*(7), 2965–2977. https://doi.org/10.1093/cercor/bhy163

Cheyette, S. J., & Piantadosi, S. T. (2020). A unified account of numerosity perception. *Nature Human Behaviour*, *4*(12), 1265–1272. https://doi.org/10.1038/s41562-020-00946-0

Chochon, F., Cohen, L., Moortele, P. F. van de, & Dehaene, S. (1999). Differential Contributions of the Left and Right Inferior Parietal Lobules to Number Processing. *Journal of Cognitive Neuroscience*, *11*(6), 617–630. https://doi.org/10.1162/089892999563689

Chomsky, N. (1988). *Language and Problems of Knowledge: The Managua Lectures* (Vol. 16, Issue 2, pp. 5–33). MIT Press.

Choo, H., & Franconeri, S. L. (2014). Enumeration of small collections violates Weber's law. *Psychonomic Bulletin & Review*, *21*(1), 93–99. https://doi.org/10.3758/s13423-013-0474-4

Chun, J., Lee, D., Lee, Y., & Cho, S. (2018). Bidirectional examination of the interaction between time and numerosity corroborates that numerosity influences time estimation but not vice versa. *Scandinavian Journal of Psychology*, *59*(3), 252–261. https://doi.org/10.1111/sjop.12445

Church, R. M., & Broadbent, H. A. (1990). Alternative representations of time, number, and rate. *Special Issue Animal Cognition*, *37*(1), 55–81. https://doi.org/10.1016/0010-0277(90)90018-F

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

Cicchini, G. M., Anobile, G., & Burr, D. C. (2014). Compressive mapping of number to space reflects dynamic encoding mechanisms, not static logarithmic transform. *Proceedings of the National Academy of Sciences*, *111*(21), 7867–7872. https://doi.org/10.1073/pnas.1402785111

Cipolotti, L., Butterworth, B., & Denes, G. (1991). A specific deficit for numbers in a case of dense acalculia. *Brain*, *114 (Pt 6)*, 2619–2637. PubMed. https://doi.org/10.1093/brain/114.6.2619

Clifford, C. W. G., Webster, M. A., Stanley, G. B., Stocker, A. A., Kohn, A., Sharpee, T. O., & Schwartz, O. (2007). Visual adaptation: Neural, psychological and computational aspects. *Vision Research*, *47*(25), 3125–3131. https://doi.org/10.1016/j.visres.2007.08.023

Clifford, C. W. G., Wyatt, A. M., Arnold, D. H., Smith, S. T., & Wenderoth, P. (2001). Orthogonal adaptation improves orientation discrimination. *Vision Research*, *41*(2), 151–159. https://doi.org/10.1016/S0042-6989(00)00248-0

Clifford, C. W., Wenderoth, P., & Spehar, B. (2000). A functional angle on some after-effects in cortical vision. *Proceedings. Biological Sciences*, *267*(1454), 1705–1710. PubMed. https://doi.org/10.1098/rspb.2000.1198

Cohen Kadosh, R., Lammertyn, J., & Izard, V. (2008). Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. *Progress in Neurobiology*, *84*(2), 132–147. https://doi.org/10.1016/j.pneurobio.2007.11.001

Cohen, Z. Z., & Henik, A. (2015). Effects of Numerosity Range on Tactile and Visual Enumeration. *Perception*, *45*(1–2), 83–98. https://doi.org/10.1177/0301006615614662

Corbett, J. E., Fischer, J., & Whitney, D. (2011). Facilitating Stable Representations: Serial Dependence in Vision. *PLOS ONE*, *6*(1), e16701. https://doi.org/10.1371/journal.pone.0016701

Cordes, S., Gelman, R., Gallistel, C. R., & Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychonomic Bulletin & Review*, *8*(4), 698–707. https://doi.org/10.3758/BF03196206

Cox, R. W. (1996). AFNI: Software for Analysis and Visualization of Functional Magnetic Resonance Neuroimages. *Computers and Biomedical Research*, *29*(3), 162–173. https://doi.org/10.1006/cbmr.1996.0014

Creelman, C. D. (1962). Human Discrimination of Auditory Duration. *The Journal of the Acoustical Society of America*, *34*(5), 582–593. https://doi.org/10.1121/1.1918172

Dakin, S. C., Tibber, M. S., Greenwood, J. A., Kingdom, F. A. A., & Morgan, M. J. (2011). A common visual metric for approximate number and density. *Proceedings of the National Academy of Sciences*, *108*(49), 19552–19557. https://doi.org/10.1073/pnas.1113195108

Dantzig, T. (1930). *Number: The Language of Science*. The Free Press.

de Hevia, M. D., Izard, V., Coubart, A., Spelke, E. S., & Streri, A. (2014). Representations of space, time, and number in neonates. *Proceedings of the National Academy of Sciences*, *111*(13), 4809–4813. https://doi.org/10.1073/pnas.1323628111

De Valois, R. L., Albrecht, D. G., & Thorell, L. G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. *Vision Research*, *22*(5), 545–559.

De Visscher, A., Noël, M.-P., Pesenti, M., & Dormal, V. (2018). Developmental Dyscalculia in Adults: Beyond Numerical Magnitude Impairment. *Journal of Learning Disabilities*, *51*(6), 600–611. https://doi.org/10.1177/0022219417732338

DeAngelis, G. C., Cumming, B. G., & Newsome, W. T. (1998). Cortical area MT and the perception of stereoscopic depth. *Nature*, *394*(6694), 677–680. https://doi.org/10.1038/29299

Dehaene, S. (1992). Varieties of numerical abilities. *Numerical Cognition*, *44*(1), 1–42. https://doi.org/10.1016/0010-0277(92)90049-N

Dehaene, S. (2001a). Précis of The Number Sense. *Mind & Language*, *16*(1), 16–36. https://doi.org/10.1111/1468-0017.00154

Dehaene, S. (2001b). Subtracting Pigeons: Logarithmic or Linear? *Psychological Science*, *12*(3), 244–246. https://doi.org/10.1111/1467-9280.00343

Dehaene, S. (2011). *The number sense: How the mind creates mathematics, Rev. And updated ed.* (pp. xxii, 316). Oxford University Press.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General*, *122*(3), 371–396. https://doi.org/10.1037/0096-3445.122.3.371

Dehaene, S., & Brannon, E. (2011). *Space, time and number in the brain: Searching for the foundations of mathematical thought*. Academic Press.

Dehaene, S., & Changeux, J.-P. (1993). Development of Elementary Numerical Abilities: A Neuronal Model. *Journal of Cognitive Neuroscience*, *5*(4), 390–407. https://doi.org/10.1162/jocn.1993.5.4.390

Dehaene, S., & Cohen, L. (1997). Cerebral Pathways for Calculation: Double Dissociation between Rote Verbal and Quantitative Knowledge of Arithmetic. *Cortex*, *33*(2), 219–250. https://doi.org/10.1016/S0010-9452(08)70002-9

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences*, *21*(8), 355–361. https://doi.org/10.1016/S0166-2236(98)01263-6

Dehaene, S., Tzourio, N., Frak, V., Raynaud, L., Cohen, L., Mehler, J., & Mazoyer, B. (1996). Cerebral activations during number multiplication and comparison: A PET study. *Neuropsychologia*, *34*(11), 1097–1106. https://doi.org/10.1016/0028-3932(96)00027-9

Demeyere, N., Rotshtein, P., & Humphreys, G. W. (2014). Common and dissociated mechanisms for estimating large and small dot arrays: Value-specific fMRI adaptation. *Human Brain Mapping*, *35*(8), 3988–4001. https://doi.org/10.1002/hbm.22453

Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. *Proceedings of the National Academy of Sciences*, *93*(24), 13494. https://doi.org/10.1073/pnas.93.24.13494

DeWind, N. K., Adams, G. K., Platt, M. L., & Brannon, E. M. (2015). Modeling the approximate number system to quantify the contribution of visual stimulus features. *Cognition*, *142*, 247–265. https://doi.org/10.1016/j.cognition.2015.05.016

Ditz, H. M., & Nieder, A. (2016). Numerosity representations in crows obey the Weber–Fechner law. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827), 20160083. https://doi.org/10.1098/rspb.2016.0083

Dormal, V., Andres, M., & Pesenti, M. (2008). Dissociation of numerosity and duration processing in the left intraparietal sulcus: A transcranial magnetic stimulation study. *Cortex*, *44*(4), 462–469. https://doi.org/10.1016/j.cortex.2007.08.011

Dormal, V., Andres, M., & Pesenti, M. (2012). Contribution of the right intraparietal sulcus to numerosity and length processing: An fMRI-guided TMS study. *Cortex*, *48*(5), 623–629. https://doi.org/10.1016/j.cortex.2011.05.019

Dormal, V., Dormal, G., Joassin, F., & Pesenti, M. (2012). A common right fronto-parietal network for numerosity and duration processing: An fMRI study. *Human Brain Mapping*, *33*(6), 1490–1501. https://doi.org/10.1002/hbm.21300

Dormal, V., & Pesenti, M. (2013). Processing numerosity, length and duration in a three-dimensional Stroop-like task: Towards a gradient of processing automaticity? *Psychological Research*, *77*(2), 116–127. https://doi.org/10.1007/s00426-012-0414-3

Dormal, V., Seron, X., & Pesenti, M. (2006). Numerosity-duration interference: A Stroop experiment. *Acta Psychologica*, *121*(2), 109–124. https://doi.org/10.1016/j.actpsy.2005.06.003

Dragoi, V., Rivadulla, C., & Sur, M. (2001). Foci of orientation plasticity in visual cortex. *Nature*, *411*(6833), 80–86. https://doi.org/10.1038/35075070

Dragoi, V., Sharma, J., Miller, E. K., & Sur, M. (2002). Dynamics of neuronal sensitivity in visual cortex and local feature discrimination. *Nature Neuroscience*, *5*(9), 883–891. https://doi.org/10.1038/nn900

Dragoi, V., Sharma, J., & Sur, M. (2000). Adaptation-Induced Plasticity of Orientation Tuning in Adult Visual Cortex. *Neuron*, *28*(1), 287–298. https://doi.org/10.1016/S0896-6273(00)00103-3

Droit-Volet, S., Clément, A., & Fayol, M. (2008). Time, number and length: Similarities and differences in discrimination in adults and children. *The Quarterly Journal of Experimental Psychology*, *61*(12), 1827–1846. https://doi.org/10.1080/17470210701743643

Dubner, R., & Zeki, S. (1971). Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey. *Brain Res*, *35*(2), 528–532. PubMed. https://doi.org/10.1016/0006-8993(71)90494-x

Dumoulin, S. O., Fracasso, A., van der Zwaag, W., Siero, J. C. W., & Petridou, N. (2018). Ultra-high field MRI: Advancing systems neuroscience towards mesoscopic human brain function. *Neuroimaging with Ultra-High Field MRI: Present and Future*, *168*, 345–357. https://doi.org/10.1016/j.neuroimage.2017.01.028

Dumoulin, S. O., & Wandell, B. A. (2008). Population receptive field estimates in human visual cortex. *NeuroImage*, *39*(2), 647–660. https://doi.org/10.1016/j.neuroimage.2007.09.034

Durgin, F. H. (1995). Texture density adaptation and the perceived numerosity and distribution of texture. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 149–169. https://doi.org/10.1037/0096-1523.21.1.149

Durgin, F. H. (2008). Texture density adaptation and visual number revisited. *Current Biology*, *18*(18), R855–R856. https://doi.org/10.1016/j.cub.2008.07.053

Duysens, J., Schaafsma, S. J., & Orban, G. A. (1996). Cortical Off Response Tuning for Stimulus Duration. *Vision Research*, *36*(20), 3243–3251. https://doi.org/10.1016/0042-6989(96)00040-5

Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., & Kleinschmidt, A. (2009). Deciphering Cortical Number Coding from Human Brain Activity Patterns. *Current Biology*, *19*(19), 1608–1615. https://doi.org/10.1016/j.cub.2009.08.047

Eger, E., Sterzer, P., Russ, M. O., Giraud, A.-L., & Kleinschmidt, A. (2003). A Supramodal Number Representation in Human Intraparietal Cortex. *Neuron*, *37*(4), 719–726. https://doi.org/10.1016/S0896-6273(03)00036-9

Ehrlich, D., Casseday, J. H., & Covey, E. (1997). Neural Tuning to Sound Duration in the Inferior Colliculus of the Big Brown Bat, *Eptesicus fuscus*. *Journal of Neurophysiology*, *77*(5), 2360–2372. https://doi.org/10.1152/jn.1997.77.5.2360

Eiselt, A.-K., & Nieder, A. (2016). Single-cell coding of sensory, spatial and numerical magnitudes in primate prefrontal, premotor and cingulate motor cortices. *Experimental Brain Research*, *234*(1), 241–254. https://doi.org/10.1007/s00221-015-4449-8

Eriksson, D., Tompa, T., & Roland, P. E. (2008). Non-Linear Population Firing Rates and Voltage Sensitive Dye Signals in Visual Areas 17 and 18 to Short Duration Stimuli. *PLoS ONE*, *3*(7), 10.

Everett, C., & Madora, K. (2012). Quantity recognition among speakers of an anumeric language. *Cognitive Science*, *36*(1), 130–141. https://doi.org/10.1111/j.1551-6709.2011.01209.x

Fechner, G. T. (1860). *Elemente der psychophysik*. Breitkopf and Härtel.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences*, *8*(7), 307–314. https://doi.org/10.1016/j.tics.2004.05.002

Ferrandez, A. M., Hugueville, L., Lehéricy, S., Poline, J. B., Marsault, C., & Pouthas, V. (2003). Basal ganglia and supplementary motor area subtend duration perception: An fMRI study. *NeuroImage*, *19*(4), 1532–1544. https://doi.org/10.1016/S1053-8119(03)00159-9

Fetterman, J. (1993). Numerosity discrimination: Both time and number matter. *Journal of Experimental Psychology. Animal Behavior Processes*, *19*(2), 149—164. https://doi.org/10.1037/0097-7403.19.2.149

Fornaciai, M., Brannon, E. M., Woldorff, M. G., & Park, J. (2017). Numerosity processing in early visual cortex. *NeuroImage*, *157*, 429–438. https://doi.org/10.1016/j.neuroimage.2017.05.069

Fornaciai, M., Cicchini, G. M., & Burr, D. C. (2016). Adaptation to number operates on perceived rather than physical numerosity. *Cognition*, *151*, 63–67. https://doi.org/10.1016/j.cognition.2016.03.006

Fornaciai, M., & Park, J. (2018). Serial dependence in numerosity perception. *Journal of Vision*, *18*(9), 15–15. https://doi.org/10.1167/18.9.15

Fornaciai, M., Togoli, I., & Arrighi, R. (2018). Motion-induced compression of perceived numerosity. *Scientific Reports*, *8*(1), 6966. https://doi.org/10.1038/s41598-018-25244-8

Frisby, J. P. (1979). *Seeing: Illusion, brain and mind*. Oxford Univ. Press. https://cds.cern.ch/record/98870

Gallace, A., Tan, H. Z., & Spence, C. (2008). Can Tactile Stimuli Be Subitised? An Unresolved Controversy within the Literature on Numerosity Judgments. *Perception*, *37*(5), 782–800. https://doi.org/10.1068/p5767

Gallistel, C. R. (1989). Animal Cognition: The Representation of Space, Time and Number. *Annual Review of Psychology*, *40*(1), 155–189. https://doi.org/10.1146/annurev.ps.40.020189.001103

Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences*, *4*(2), 59–65. https://doi.org/10.1016/S1364-6613(99)01424-2

Gardner, E. P., Babu, K. S., Ghosh, S., Sherwood, A., & Chen, J. (2007). Neurophysiology of Prehension. III. Representation of Object Features in Posterior Parietal Cortex of the Macaque Monkey. *Journal of Neurophysiology*, *98*(6), 3708–3730. https://doi.org/10.1152/jn.00609.2007

Gebuis, T., Cohen Kadosh, R., & Gevers, W. (2016). Sensory-integration system rather than approximate number system underlies numerosity processing: A critical review. *Acta Psychologica*, *171*, 17–35. https://doi.org/10.1016/j.actpsy.2016.09.003

Gebuis, T., & Reynvoet, B. (2012). Continuous visual properties explain neural responses to nonsymbolic number. *Psychophysiology*, *49*(11), 1649–1659. https://doi.org/10.1111/j.1469-8986.2012.01461.x

Ghose, G. M., & Maunsell, J. H. R. (2002). Attentional modulation in visual cortex depends on task timing. *Nature*, *419*(6907), 616–620. https://doi.org/10.1038/nature01057

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. *Annals of the New York Academy of Sciences*, *423*, 52–77. https://doi.org/10.1111/j.1749-6632.1984.tb23417.x

Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, *20*(5), 453–467. https://doi.org/10.1037/h0059826

Gilaie-Dotan, S., Rees, G., Butterworth, B., & Cappelletti, M. (2014). Impaired Numerical Ability Affects Supra-Second Time Estimation. *Timing & Time Perception*, *2*(2), 169–187. https://doi.org/10.1163/22134468-00002026

Giurfa, M. (2019). An Insect's Sense of Number. *Trends in Cognitive Sciences*, *23*(9), 720–722. https://doi.org/10.1016/j.tics.2019.06.010

Gordon, P. (2004). Numerical Cognition Without Words: Evidence from Amazonia. *Science*, *306*(5695), 496. https://doi.org/10.1126/science.1094492

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*(1), 14–23. https://doi.org/10.1016/j.tics.2005.11.006

Grondin, S. (2010). Timing and time perception: A review of recent behavioral and neuroscience findings and theoretical directions. *Attention Perception & Psychophysics*, *72*(3), 561–582. https://doi.org/10.3758/APP.72.3.561

Grondin, S. (2014). About the (Non)scalar Property for Time Perception. In H. Merchant & V. de Lafuente (Eds.), *Neurobiology of Interval Timing* (pp. 17–32). Springer New York. https://doi.org/10.1007/978-1-4939-1782-2_2

Halberda, J., & Feigenson, L. (2008). Developmental change in the acuity of the "number sense": The approximate number system in 3-, 4-, 5-, and 6-year-olds and adults. *Developmental Psychology*, *44*(5), 1457–1465. https://doi.org/10.1037/a0012682

Hamamouche, K., & Cordes, S. (2019). Number, time, and space are not singularly represented: Evidence against a common magnitude system beyond early childhood. *Psychonomic Bulletin & Review*, *26*(3), 833–854. https://doi.org/10.3758/s13423-018-1561-3

Harrington, D. L., Haaland, K. Y., & Knight, R. T. (1998). Cortical Networks Underlying Mechanisms of Time Perception. *The Journal of Neuroscience*, *18*(3), 1085–1095. https://doi.org/10.1523/JNEUROSCI.18-03-01085.1998

Harvey, B. M., & Dumoulin, S. O. (2017a). A network of topographic numerosity maps in human association cortex. *Nature Human Behaviour*, *1*(2), 0036. https://doi.org/10.1038/s41562-016-0036

Harvey, B. M., & Dumoulin, S. O. (2017b). Can responses to basic non-numerical visual features explain neural numerosity responses? *NeuroImage*, *149*, 200–209. https://doi.org/10.1016/j.neuroimage.2017.02.012

Harvey, B. M., & Dumoulin, S. O. (2018). Data describing the accuracy of non-numerical visual features in predicting fMRI responses to numerosity. *Data in Brief*, *16*, 193–205. https://doi.org/10.1016/j.dib.2017.11.022

Harvey, B. M., Dumoulin, S. O., Fracasso, A., & Paul, J. M. (2020). A Network of Topographic Maps in Human Association Cortex Hierarchically Transforms Visual Timing-Selective Responses. *Current Biology*, *30*(8), 1424-1434.e6. https://doi.org/10.1016/j.cub.2020.01.090

Harvey, B. M., Ferri, S., & Orban, G. A. (2017). Comparing Parietal Quantity-Processing Mechanisms between Humans and Macaques. *Trends in Cognitive Sciences*, *21*(10), 779–793. https://doi.org/10.1016/j.tics.2017.07.002

Harvey, B. M., Fracasso, A., Petridou, N., & Dumoulin, S. O. (2015). Topographic representations of object size and relationships with numerosity reveal generalized quantity processing in human parietal cortex. *Proceedings of the National Academy of Sciences*, *112*(44), 13525–13530. https://doi.org/10.1073/pnas.1515414112

Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic Representation of Numerosity in the Human Parietal Cortex. *Science*, *341*(6150), 1123–1126. https://doi.org/10.1126/science.1239052

Hauser, M. D., Tsao, F., Garcia, P., & Spelke, E. S. (2003). Evolutionary foundations of number: Spontaneous representation of numerical magnitudes by cotton–top tamarins. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1523), 1441–1446. https://doi.org/10.1098/rspb.2003.2414

Hawken, M. J., Shapley, R. M., & Grosof, D. H. (1996). Temporal-frequency selectivity in monkey visual cortex. *Visual Neuroscience*, *13*(3), 477–492. https://doi.org/10.1017/S0952523800008154

Hayashi, M. J., Ditye, T., Harada, T., Hashiguchi, M., Sadato, N., Carlson, S., Walsh, V., & Kanai, R. (2015). Time Adaptation Shows Duration Selectivity in the Human Parietal Cortex. *PLOS Biology*, *13*(9), e1002262. https://doi.org/10.1371/journal.pbio.1002262

Hayashi, M. J., & Ivry, R. B. (2020). Duration Selectivity in Right Parietal Cortex Reflects the Subjective Experience of Time. *The Journal of Neuroscience*, *40*(40), 7749. https://doi.org/10.1523/JNEUROSCI.0078-20.2020

Hayashi, M. J., Kanai, R., Tanabe, H. C., Yoshida, Y., Carlson, S., Walsh, V., & Sadato, N. (2013). Interaction of Numerosity and Time in Prefrontal and Parietal Cortex. *Journal of Neuroscience*, *33*(3), 883–893. https://doi.org/10.1523/JNEUROSCI.6257-11.2013

Hayashi, M. J., Kantele, M., Walsh, V., Carlson, S., & Kanai, R. (2014). Dissociable Neuroanatomical Correlates of Subsecond and Suprasecond Time Perception. *Journal of Cognitive Neuroscience*, *26*(8), 1685–1693. https://doi.org/10.1162/jocn_a_00580

Hayashi, M. J., Valli, A., & Carlson, S. (2013). Numerical quantity affects time estimation in the suprasecond range. *Neuroscience Letters*, *543*, 7–11. https://doi.org/10.1016/j.neulet.2013.02.054

He, J., Hashikawa, T., Ojima, H., & Kinouchi, Y. (1997). Temporal Integration and Duration Tuning in the Dorsal Zone of Cat Auditory Cortex. *The Journal of Neuroscience*, *17*(7), 2615–2625. https://doi.org/10.1523/JNEUROSCI.17-07-02615.1997

He, L., Zhou, K., Zhou, T., He, S., & Chen, L. (2015). Topology-defined units in numerosity perception. *Proceedings of the National Academy of Sciences*, *112*(41), E5647–E5655. https://doi.org/10.1073/pnas.1512408112

Heron, J., Aaen-Stockdale, C., Hotchkiss, J., Roach, N. W., McGraw, P. V., & Whitaker, D. (2012). Duration channels mediate human time perception. *Proceedings of the Royal Society B-Biological Sciences*, *279*(1729), 690–698. https://doi.org/10.1098/rspb.2011.1131

Heron, J., Fulcher, C., Collins, H., Whitaker, D., & Roach, N. W. (2019). Adaptation reveals multi-stage coding of visual duration. *Scientific Reports*, *9*(1), 3016. https://doi.org/10.1038/s41598-018-37614-3

Heron, J., Hotchkiss, J., Aaen-Stockdale, C., Roach, N. W., & Whitaker, D. (2013). A neural hierarchy for illusions of time: Duration adaptation precedes multisensory integration. *Journal of Vision*, *13*(14), 4. https://doi.org/10.1167/13.14.4

Heron, J., Roach, N. W., Hanson, J. V. M., McGraw, P. V., & Whitaker, D. (2012). Audiovisual time perception is spatially specific. *Experimental Brain Research*, *218*(3), 477–485. https://doi.org/10.1007/s00221-012-3038-3

Hershenson, M. (1989). Duration, time constant, and decay of the linear motion aftereffect as a function of inspection duration. *Perception & Psychophysics*, *45*(3), 251–257. https://doi.org/10.3758/BF03210704

Hofstetter, S., Cai, Y., Harvey, B. M., & Dumoulin, S. O. (2021). Topographic maps representing haptic numerosity reveals distinct sensory representations in supramodal networks. *Nature Communications*, *12*(1), 221. https://doi.org/10.1038/s41467-020-20567-5

Hofstetter, S., & Dumoulin, S. O. (2021). Tuned neural responses to haptic numerosity in the putamen. *NeuroImage*, 118178. https://doi.org/10.1016/j.neuroimage.2021.118178

Hollingworth, H. L. (1910). The Central Tendency of Judgment. *The Journal of Philosophy, Psychology and Scientific Methods*, *7*(17), 461–469. JSTOR. https://doi.org/10.2307/2012819

Holmes, G. (1918). DISTURBANCES OF VISION BY CEREBRAL LESIONS. *The British Journal of Ophthalmology*, *2*(7), 353–384. PubMed. https://doi.org/10.1136/bjo.2.7.353

Horton, J. C., Dagi, L. R., McCrane, E. P., & de Monasterio, F. M. (1990). Arrangement of Ocular Dominance Columns in Human Visual Cortex. *Archives of Ophthalmology*, *108*(7), 1025–1031. https://doi.org/10.1001/archopht.1990.01070090127054

Howard, S. R., Avarguès-Weber, A., Garcia, J. E., Greentree, A. D., & Dyer, A. G. (2018). Numerical ordering of zero in honey bees. *Science*, *360*(6393), 1124–1126. https://doi.org/10.1126/science.aar4975

Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, *6*(6), 435–448. https://doi.org/10.1038/nrn1684

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of Physiology*, *160*(1), 106–154. https://doi.org/10.1113/jphysiol.1962.sp006837

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *The Journal of Physiology*, *195*(1), 215–243.

Inouye, T. (1909). *Die Sehstörungen bei Schussverletzungen der kortikalen Sehsphäre: Nach Beobachtungen an Verwundeten der letzten japanischen Kriege*. Engelmann.

Iuculano, T., Tang, J., Hall, C. W. B., & Butterworth, B. (2008). Core information processing deficits in developmental dyscalculia and low numeracy. *Developmental Science*, *11*(5), 669–680. https://doi.org/10.1111/j.1467-7687.2008.00716.x

Ivry, R. B. (1996). The representation of temporal information in perception and motor control. *Current Opinion in Neurobiology*, *6*(6), 851–857. https://doi.org/10.1016/S0959-4388(96)80037-7

Ivry, R. B., & Schlerf, J. E. (2008). Dedicated and intrinsic models of time perception. *Trends in Cognitive Sciences*, *12*(7), 273–280. https://doi.org/10.1016/j.tics.2008.04.002

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences*, *106*(25), 10382–10385. https://doi.org/10.1073/pnas.0812142106

Jacob, S. N., & Nieder, A. (2009). Tuning to non-symbolic proportions in the human frontoparietal cortex: Representation of proportions in the human brain. *European Journal of Neuroscience*, *30*(7), 1432–1442. https://doi.org/10.1111/j.1460-9568.2009.06932.x

Jarosz, A. F., & Wiley, J. (2014). What are the odds? A practical guide to computing and reporting bayes factors. *Journal of Problem Solving*, *7*(1), 2–9. Scopus. https://doi.org/10.7771/1932-6246.1167

JASP Team. (2019). *JASP (Version 0.11.1)[Computer software]*. https://jasp-stats.org/

Javadi, A. H., & Aichelburg, C. (2012). When Time and Numerosity Interfere: The Longer the More, and the More the Longer. *PLoS ONE*, *7*(7), e41496. https://doi.org/10.1371/journal.pone.0041496

Javadi, A. H., Brunec, I. K., Walsh, V., Penny, W. D., & Spiers, H. J. (2014). Transcranial electrical brain stimulation modulates neuronal tuning curves in perception of numerosity and duration. *NeuroImage*, *102*, 451–457. https://doi.org/10.1016/j.neuroimage.2014.08.016

Jazayeri, M., & Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nature Neuroscience*, *13*(8), 1020–1026. https://doi.org/10.1038/nn.2590

Jazayeri, M., & Shadlen, M. N. (2015). A Neural Mechanism for Sensing and Reproducing a Time Interval. *Current Biology*, *25*(20), 2599–2609. https://doi.org/10.1016/j.cub.2015.08.038

Jin, D. Z., Dragoi, V., Sur, M., & Seung, H. S. (2005). Tilt Aftereffect and Adaptation-Induced Changes in Orientation Tuning in Visual Cortex. *Journal of Neurophysiology*, *94*(6), 4038–4050. https://doi.org/10.1152/jn.00571.2004

Jin, D. Z., Fujii, N., & Graybiel, A. M. (2009). Neural representation of time in cortico-basal ganglia circuits. *Proceedings of the National Academy of Sciences*, *106*(45), 19156–19161. https://doi.org/10.1073/pnas.0909881106

Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially Localized Distortions of Event Time. *Current Biology*, *16*(5), 472–479. https://doi.org/10.1016/j.cub.2006.01.032

Jones, S. M., Pearson, J., DeWind, N. K., Paulsen, D., Tenekedjieva, A.-M., & Brannon, E. M. (2014). Lemurs and macaques show similar numerical sensitivity. *Animal Cognition*, *17*(3), 503–515. https://doi.org/10.1007/s10071-013-0682-3

Jordan, K. E., & Brannon, E. M. (2006). Weber's Law influences numerical representations in rhesus macaques (Macaca mulatta). *Animal Cognition*, *9*(3), 159–172. https://doi.org/10.1007/s10071-006-0017-8

Kaas, J. H., & Hackett, T. A. (2000). Subdivisions of auditory cortex and processing streams in primates. *Proceedings of the National Academy of Sciences*, *97*(22), 11793. https://doi.org/10.1073/pnas.97.22.11793

Kappers, A. M. L., & Bergmann Tiest, W. M. (2014). Influence of Shape on the Haptic Size Aftereffect. *PLOS ONE*, *9*(2), e88729. https://doi.org/10.1371/journal.pone.0088729

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The discrimination of visual number. *The American Journal of Psychology*, *62*, 498–525. https://doi.org/10.2307/1418556

Kersey, A. J., & Cantlon, J. F. (2017). Neural Tuning to Numerosity Relates to Perceptual Tuning in 3–6-Year-Old Children. *The Journal of Neuroscience*, *37*(3), 512. https://doi.org/10.1523/JNEUROSCI.0065-16.2016

Kim, G., Jang, J., Baek, S., Song, M., & Paik, S.-B. (2021). Visual number sense in untrained deep neural networks. *Science Advances*, *7*(1), eabd6127. PubMed. https://doi.org/10.1126/sciadv.abd6127

Klein, B. P., Harvey, B. M., & Dumoulin, S. O. (2014). Attraction of Position Preference by Spatial Attention throughout Human Visual Cortex. *Neuron*, *84*(1), 227–237. https://doi.org/10.1016/j.neuron.2014.08.047

Klein, B. P., Paffen, C. L. E., Pas, S. F. te, & Dumoulin, S. O. (2016). Predicting bias in perceived position using attention field models. *Journal of Vision*, *16*(7), 15. https://doi.org/10.1167/16.7.15

Kleiner, M., Brainard, D. H., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception*, *36*, 1–16. https://doi.org/10.1068/v070821

Kohn, A. (2007). Visual Adaptation: Physiology, Mechanisms, and Functional Benefits. *Journal of Neurophysiology*, *97*(5), 3155–3164. https://doi.org/10.1152/jn.00086.2007

Kohn, A., & Movshon, J. A. (2004). Adaptation changes the direction tuning of macaque MT neurons. *Nature Neuroscience*, *7*(7), 764–772. https://doi.org/10.1038/nn1267

Krekelberg, B., Boynton, G. M., & van Wezel, R. J. A. (2006). Adaptation: From single cells to BOLD signals. *Trends in Neurosciences*, *29*(5), 250–256. https://doi.org/10.1016/j.tins.2006.02.008

Krekelberg, B., van Wezel, R. J. A., & Albright, T. D. (2006). Adaptation in Macaque MT Reduces Perceived Speed and Improves Speed Discrimination. *Journal of Neurophysiology*, *95*(1), 255–270. https://doi.org/10.1152/jn.00750.2005

Kristensen, S., Fracasso, A., Dumoulin, S. O., Almeida, J., & Harvey, B. M. (2021). Size constancy affects the perception and parietal neural representation of object size. *NeuroImage*, *232*, 117909. https://doi.org/10.1016/j.neuroimage.2021.117909

Krusche, P., Uller, C., & Dicke, U. (2010). Quantity discrimination in salamanders. *Journal of Experimental Biology*, *213*(11), 1822–1828. https://doi.org/10.1242/jeb.039297

Kutter, E. F., Bostroem, J., Elger, C. E., Mormann, F., & Nieder, A. (2018). Single Neurons in the Human Brain Encode Numbers. *Neuron*, *100*(3), 753-761.e4. https://doi.org/10.1016/j.neuron.2018.08.036

Lambrechts, A., Walsh, V., & van Wassenhove, V. (2013). Evidence Accumulation in the Magnitude System. *PLoS ONE*, *8*(12), e82122. https://doi.org/10.1371/journal.pone.0082122

Larsson, J., Solomon, S. G., & Kohn, A. (2016). FMRI adaptation revisited. *Cortex*, *80*, 154–160. https://doi.org/10.1016/j.cortex.2015.10.026

Lasne, G., Piazza, M., Dehaene, S., Kleinschmidt, A., & Eger, E. (2019). Discriminability of numerosity-evoked fMRI activity patterns in human intra-parietal cortex reflects behavioral numerical acuity. *Architecture of Mathematical Cognition*, *114*, 90–101. https://doi.org/10.1016/j.cortex.2018.03.008

Leibovich, T., Katzin, N., Harel, M., & Henik, A. (2017). From "sense of number" to "sense of magnitude": The role of continuous magnitudes in numerical cognition. *Behavioral and Brain Sciences*, *40*, e164. Cambridge Core. https://doi.org/10.1017/S0140525X16000960

Leon, M. I., & Shadlen, M. N. (2003). Representation of Time by Neurons in the Posterior Parietal Cortex of the Macaque. *Neuron*, *38*(2), 317–327. https://doi.org/10.1016/S0896-6273(03)00185-5

Lewis, P. A., & Miall, R. C. (2009). The precision of temporal judgement: Milliseconds, many minutes, and beyond. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1525), 1897–1905. https://doi.org/10.1098/rstb.2009.0020

Li, B., Chen, L., & Fang, F. (2019). Somatotopic representation of tactile duration: Evidence from tactile duration aftereffect. *Behavioural Brain Research*, *371*, 111954. https://doi.org/10.1016/j.bbr.2019.111954

Li, B., Chen, Y., Xiao, L., Liu, P., & Huang, X. (2017). Duration adaptation modulates EEG correlates of subsequent temporal encoding. *NeuroImage*, *147*, 143–151. https://doi.org/10.1016/j.neuroimage.2016.12.015

Li, B., Yuan, X., Chen, Y., Liu, P., & Huang, X. (2015). Visual duration aftereffect is position invariant. *Frontiers in Psychology*, *6*, 1536. https://doi.org/10.3389/fpsyg.2015.01536

Lipton, J. S., & Spelke, E. S. (2003). Origins of Number Sense: Large-Number Discrimination in Human Infants. *Psychological Science*, *14*(5), 396–401. https://doi.org/10.1111/1467-9280.01453

Liu, W., Zhang, Z.-J., Li, B.-C., Zhao, Y.-J., & Tang, Y. (2015). Numerosity adaptation along the Y-Axis affects numerosity perception along the X-Axis: Does numerosity adaptation activate MNLs? *Attention, Perception, & Psychophysics*, *77*(4), 1358–1370. https://doi.org/10.3758/s13414-015-0863-z

Liu, W., Zhang, Z.-J., Zhao, Y.-J., Li, B.-C., & Wang, M. (2017). Distinct mechanisms in the numerosity processing of random and regular dots. *Acta Psychologica*, *174*, 17–30. https://doi.org/10.1016/j.actpsy.2017.01.006

Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*(4), 476–490. https://doi.org/10.3758/BF03210951

Logothetis, N. K. (2003). The Underpinnings of the BOLD Functional Magnetic Resonance Imaging Signal. *The Journal of Neuroscience*, *23*(10), 3963. https://doi.org/10.1523/JNEUROSCI.23-10-03963.2003

Logothetis, N. K., & Wandell, B. A. (2004). Interpreting the BOLD Signal. *Annual Review of Physiology*, *66*(1), 735–769. https://doi.org/10.1146/annurev.physiol.66.082602.092845

Long, G. M., & Beaton, R. J. (1981). The effects of stimulus numerosity, retinal location, and rod contrast on perceived duration of brief visual stimuli. *Perception & Psychophysics*, *29*(4), 389–394. https://doi.org/10.3758/BF03207349

Lourenco, S. F., & Longo, M. R. (2010). General Magnitude Representation in Human Infants. *Psychological Science*, *21*(6), 873–881. https://doi.org/10.1177/0956797610370158

Lourenco, S. F., & Longo, M. R. (2011). Chapter 15—Origins and Development of Generalized Magnitude Representation. In S. Dehaene & E. M. Brannon (Eds.), *Space, Time and Number in the Brain* (pp. 225–244). Academic Press. https://doi.org/10.1016/B978-0-12-385948-8.00015-3

Maarseveen, J., Hogendoorn, H., Verstraten, F. A. J., & Paffen, C. L. E. (2017). An investigation of the spatial selectivity of the duration after-effect. *Vision Research*, *130*, 67–75. https://doi.org/10.1016/j.visres.2016.11.003

Maarseveen, J., Paffen, C. L. E., Verstraten, F. A. J., & Hogendoorn, H. (2019). The duration aftereffect does not reflect adaptation to perceived duration. *PLOS ONE*, *14*(3), e0213163. https://doi.org/10.1371/journal.pone.0213163

Magnussen, S., & Johnsen, T. (1986). Temporal aspects of spatial adaptation. A study of the tilt aftereffect. *Vision Research*, *26*(4), 661–672. https://doi.org/10.1016/0042-6989(86)90014-3

Mandler, G., & Shebo, B. J. (1982). Subitizing: An analysis of its component processes. *Journal of Experimental Psychology: General*, *111*(1), 1–22. https://doi.org/10.1037/0096-3445.111.1.1

Marcos, E., Tsujimoto, S., & Genovesio, A. (2017). Independent coding of absolute duration and distance magnitudes in the prefrontal cortex. *Journal of Neurophysiology*, *117*(1), 195–203. https://doi.org/10.1152/jn.00245.2016

Martin, B., Wiener, M., & van Wassenhove, V. (2017). A Bayesian Perspective on Accumulation in the Magnitude System. *Scientific Reports*, *7*(1), 630. https://doi.org/10.1038/s41598-017-00680-0

Matell, M. S. (2014). Searching for the holy grail: Temporally informative firing patterns in the rat. *Advances in Experimental Medicine and Biology*, *829*, 209–234. PubMed. https://doi.org/10.1007/978-1-4939-1782-2_12

Matell, M. S., & Meck, W. H. (2004). Cortico-striatal circuits and interval timing: Coincidence detection of oscillatory processes. *Neuroimaging of Interval Timing*, *21*(2), 139–170. https://doi.org/10.1016/j.cogbrainres.2004.06.012

Mauk, M. D., & Buonomano, D. V. (2004). THE NEURAL BASIS OF TEMPORAL PROCESSING. *Annual Review of Neuroscience*, *27*(1), 307–340. https://doi.org/10.1146/annurev.neuro.27.070203.144247

Mazzocco, M. M. M., Feigenson, L., & Halberda, J. (2011). Impaired Acuity of the Approximate Number System Underlies Mathematical Learning Disability (Dyscalculia). *Child Development*, *82*(4), 1224–1237. https://doi.org/10.1111/j.1467-8624.2011.01608.x

Meck, W., & Church, R. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes*, *9*(3), 320–334. https://doi.org/10.1037/0097-7403.9.3.320

Meck, W., Church, R., & Gibbon, J. (1985). Temporal integration in duration and number discrimination. *Journal of Experimental Psychology: Animal Behavior Processes*, *11*(4), 591–597. https://doi.org/10.1037/0097-7403.11.4.591

Mendelson, J. R., & Cynader, M. S. (1985). Sensitivity of cat primary auditory cortex (AI) neurons to the direction and rate of frequency modulation. *Brain Research*, *327*(1), 331–335. https://doi.org/10.1016/0006-8993(85)91530-6

Menon, R. S., Ogawa, S., Strupp, J. P., & Uğurbil, K. (1997). Ocular Dominance in Human V1 Demonstrated by Functional Magnetic Resonance Imaging. *Journal of Neurophysiology*, *77*(5), 2780–2787. https://doi.org/10.1152/jn.1997.77.5.2780

Merchant, H., Pérez, O., Zarco, W., & Gámez, J. (2013). Interval Tuning in the Primate Medial Premotor Cortex as a General Timing Mechanism. *Journal of Neuroscience*, *33*(21), 9082–9096. https://doi.org/10.1523/JNEUROSCI.5513-12.2013

Merchant, H., Zarco, W., & Prado, L. (2008). Do We Have a Common Mechanism for Measuring Time in the Hundreds of Millisecond Range? Evidence From Multiple-Interval Timing Tasks. *Journal of Neurophysiology*, *99*(2), 939–949. https://doi.org/10.1152/jn.01225.2007

Miletto Petrazzini, M. E., Agrillo, C., Izard, V., & Bisazza, A. (2016). Do humans (Homo sapiens) and fish (Pterophyllum scalare) make similar numerosity judgments? *Journal of Comparative Psychology*, *130*(4), 380–390. https://doi.org/10.1037/com0000045

Mita, A., Mushiake, H., Shima, K., Matsuzaka, Y., & Tanji, J. (2009). Interval time coding by neurons in the presupplementary and supplementary motor areas. *Nature Neuroscience*, *12*(4), 502–507. https://doi.org/10.1038/nn.2272

Mollon, D. J. (1974). After-effects and the brain. *New Scientist*, *61*(886), 479–482.

Morris, S. B., & DeShon, R. P. (2002). Combining effect size estimates in meta-analysis with repeated measures and independent-groups designs. *Psychological Methods*, *7*(1), 105–125. https://doi.org/10.1037/1082-989X.7.1.105

Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience*, *8*(7), 950–954. https://doi.org/10.1038/nn1488

Motala, A., Heron, J., McGraw, P. V., Roach, N. W., & Whitaker, D. (2018). Rate after-effects fail to transfer cross-modally: Evidence for distributed sensory timing mechanisms. *Scientific Reports*, *8*(1), 924. https://doi.org/10.1038/s41598-018-19218-z

Movshon, J. A., & Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature*, *278*(5707), 850–852. https://doi.org/10.1038/278850a0

Müller, J. R., Metha, A. B., Krauskopf, J., & Lennie, P. (1999). Rapid adaptation in visual cortex to the structure of images. *Science*, *285*(5432), 1405–1408.

Murai, Y., & Yotsumoto, Y. (2016). Timescale- and Sensory Modality-Dependency of the Central Tendency of Time Perception. *PLOS ONE*, *11*(7), e0158921. https://doi.org/10.1371/journal.pone.0158921

Murai, Y., & Yotsumoto, Y. (2018). Optimal multisensory integration leads to optimal time estimation. *Scientific Reports*, *8*(1), 13068. https://doi.org/10.1038/s41598-018-31468-5

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the Shape, Size, and Orientation of Objects for Grasping in Neurons of Monkey Parietal Area AIP. *Journal of Neurophysiology*, *83*(5), 2580–2601. https://doi.org/10.1152/jn.2000.83.5.2580

Nasr, K., Viswanathan, P., & Nieder, A. (2019). Number detectors spontaneously emerge in a deep neural network designed for visual object recognition. *Science Advances*, *5*(5), eaav7903. https://doi.org/10.1126/sciadv.aav7903

Needham, J. G. (1934). The time-error in comparison judgments. *Psychological Bulletin*, *31*(4), 229–243. https://doi.org/10.1037/h0070945

Nemeh, F., Humberstone, J., Yates, M. J., & Reeve, R. A. (2018). Non-symbolic magnitudes are represented spatially: Evidence from a non-symbolic SNARC task. *PLOS ONE*, *13*(8), e0203019. https://doi.org/10.1371/journal.pone.0203019

Nieder, A. (2012). Supramodal numerosity selectivity of neurons in primate prefrontal and posterior parietal cortices. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(29), 11860–11865. https://doi.org/10.1073/pnas.1204580109

Nieder, A. (2016). The neuronal code for number. *Nature Reviews Neuroscience*, *17*(6), 366–382. https://doi.org/10.1038/nrn.2016.40

Nieder, A. (2020a). Neural constraints on human number concepts. *Current Opinion in Neurobiology*, *60*, 28–36. https://doi.org/10.1016/j.conb.2019.10.003

Nieder, A. (2020b). The Adaptive Value of Numerical Competence. *Trends in Ecology & Evolution*, *35*(7), 605–617. https://doi.org/10.1016/j.tree.2020.02.009

Nieder, A. (2021). The Evolutionary History of Brains for Numbers. *Trends in Cognitive Sciences*, *25*(7), 608–621. https://doi.org/10.1016/j.tics.2021.03.012

Nieder, A., & Dehaene, S. (2009). Representation of Number in the Brain. *Annual Review of Neuroscience*, *32*(1), 185–208. https://doi.org/10.1146/annurev.neuro.051508.135550

Nieder, A., Freedman, D. J., & Miller, E. K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. *Science*, *297*(5587), 1708–1711. https://doi.org/10.1126/science.1072493

Nieder, A., & Merten, K. (2007). A Labeled-Line Code for Small and Large Numerosities in the Monkey Prefrontal Cortex. *Journal of Neuroscience*, *27*(22), 5986–5993. https://doi.org/10.1523/JNEUROSCI.1056-07.2007

Nieder, A., & Miller, E. K. (2003). Coding of Cognitive Magnitude: Compressed Scaling of Numerical Information in the Primate Prefrontal Cortex. *Neuron*, *37*(1), 149–157. https://doi.org/10.1016/S0896-6273(02)01144-3

Nieder, A., & Miller, E. K. (2004a). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences*, *101*(19), 7457–7462. https://doi.org/10.1073/pnas.0402239101

Nieder, A., & Miller, E. K. (2004b). Analog Numerical Representations in Rhesus Monkeys: Evidence for Parallel Processing. *Journal of Cognitive Neuroscience*, *16*(5), 889–901. https://doi.org/10.1162/089892904970807

Park, J., DeWind, N. K., Woldorff, M. G., & Brannon, E. M. (2016). Rapid and Direct Encoding of Numerosity in the Visual Stream. *Cerebral Cortex*, *26*(2), 748–763. https://doi.org/10.1093/cercor/bhv017

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442. https://doi.org/10.1163/156856897X00366

Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain: A Journal of Neurology*, *60*, 389–443. https://doi.org/10.1093/brain/60.4.389

Pérez-González, D., Malmierca, M. S., Moore, J. M., Hernández, O., & Covey, E. (2006). Duration Selective Neurons in the Inferior Colliculus of the Rat: Topographic Distribution and Relation of Duration Sensitivity to Other Response Properties. *Journal of Neurophysiology*, *95*(2), 823–836. https://doi.org/10.1152/jn.00741.2005

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Special Issue: Space, Time and Number*, *14*(12), 542–551. https://doi.org/10.1016/j.tics.2010.09.008

Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., Lucangeli, D., Dehaene, S., & Zorzi, M. (2010). Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition*, *116*(1), 33–41. https://doi.org/10.1016/j.cognition.2010.03.012

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & 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

Pica, P., Lemer, C., Izard, V., & Dehaene, S. (2004). Exact and Approximate Arithmetic in an Amazonian Indigene Group. *Science*, *306*(5695), 499. https://doi.org/10.1126/science.1102085

Pinel, P., Dehaene, S., Rivière, D., & LeBihan, D. (2001). Modulation of Parietal Activation by Semantic Distance in a Number Comparison Task. *NeuroImage*, *14*(5), 1013–1026. https://doi.org/10.1006/nimg.2001.0913

Pinheiro-Chagas, P., Wood, G., Knops, A., Krinzinger, H., Lonnemann, J., Starling-Alves, I., Willmes, K., & Haase, V. G. (2014). In How Many Ways is the Approximate Number System Associated with Exact Calculation? *PLOS ONE*, *9*(11), e111155. https://doi.org/10.1371/journal.pone.0111155

Plaisier, M. A., Bergmann Tiest, W. M., & Kappers, A. M. L. (2009). One, two, three, many – Subitizing in active touch. *Acta Psychologica*, *131*(2), 163–170. https://doi.org/10.1016/j.actpsy.2009.04.003

Pomè, A., Anobile, G., Cicchini, G. M., & Burr, D. C. (2019). Different reaction-times for subitizing, estimation, and texture. *Journal of Vision*, *19*(6), 14–14. https://doi.org/10.1167/19.6.14

Pooresmaeili, A., Arrighi, R., Biagi, L., & Morrone, M. C. (2013). Blood Oxygen Level-Dependent Activation of the Primary Visual Cortex Predicts Size Adaptation Illusion. *The Journal of Neuroscience*, *33*(40), 15999. https://doi.org/10.1523/JNEUROSCI.1770-13.2013

Pouthas, V., George, N., Poline, J.-B., Pfeuty, M., VandeMoorteele, P.-F., Hugueville, L., Ferrandez, A.-M., Lehéricy, S., LeBihan, D., & Renault, B. (2005). Neural network involved in time perception: An fMRI study comparing long and short interval estimation. *Human Brain Mapping*, *25*(4), 433–441. https://doi.org/10.1002/hbm.20126

Protopapa, F., Hayashi, M. J., Kulashekhar, S., van der Zwaag, W., Battistella, G., Murray, M. M., Kanai, R., & Bueti, D. (2019). Chronotopic maps in human supplementary motor area. *PLOS Biology*, *17*(3), e3000026. https://doi.org/10.1371/journal.pbio.3000026

Repp, B. H. (2007). Perceiving the numerosity of rapidly occurring auditory events in metrical and nonmetrical contexts. *Perception & Psychophysics*, *69*(4), 529–543. https://doi.org/10.3758/BF03193910

Revkin, S. K., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (2008). Does Subitizing Reflect Numerical Estimation? *Psychological Science*, *19*(6), 607–614. https://doi.org/10.1111/j.1467-9280.2008.02130.x

Riggs, K. J., Ferrand, L., Lancelin, D., Fryziel, L., Dumur, G., & Simpson, A. (2006). Subitizing in Tactile Perception. *Psychological Science*, *17*(4), 271–272. https://doi.org/10.1111/j.1467-9280.2006.01696.x

Roggeman, C., Santens, S., Fias, W., & Verguts, T. (2011). Stages of Nonsymbolic Number Processing in Occipitoparietal Cortex Disentangled by fMRI Adaptation. *Journal of Neuroscience*, *31*(19), 7168–7173. https://doi.org/10.1523/JNEUROSCI.4503-10.2011

Roland, P. E., & Friberg, L. (1985). Localization of cortical areas activated by thinking. *Journal of Neurophysiology*, *53*(5), 1219–1243. https://doi.org/10.1152/jn.1985.53.5.1219

Romo, R., Hernández, A., Zainos, A., & Salinas, E. (1998). Somatosensory discrimination based on cortical microstimulation. *Nature*, *392*(6674), 387–390. https://doi.org/10.1038/32891

Ross, J., & Burr, D. C. (2010). Vision senses number directly. *Journal of Vision*, *10*(2), 10–10. https://doi.org/10.1167/10.2.10

Rousselle, L., & Noël, M.-P. (2007). Basic numerical skills in children with mathematics learning disabilities: A comparison of symbolic vs non-symbolic number magnitude processing. *Cognition*, *102*(3), 361–395. https://doi.org/10.1016/j.cognition.2006.01.005

Saenz, M., & Langers, D. R. M. (2014). Tonotopic mapping of human auditory cortex. *Human Auditory NeuroImaging*, *307*, 42–52. https://doi.org/10.1016/j.heares.2013.07.016

Salzman, C. D., Britten, K. H., & Newsome, W. T. (1990). Cortical microstimulation influences perceptual judgements of motion direction. *Nature*, *346*(6280), 174–177. https://doi.org/10.1038/346174a0

Saunders, J. A., & Backus, B. T. (2006). Perception of surface slant from oriented textures. *Journal of Vision*, *6*(9), 3–3. https://doi.org/10.1167/6.9.3

Sawamura, H., Shima, K., & Tanji, J. (2002). Numerical representation for action in the parietal cortex of the monkey. *Nature*, *415*(6874), 918–922. https://doi.org/10.1038/415918a

Scarf, D., Hayne, H., & Colombo, M. (2011). Pigeons on Par with Primates in Numerical Competence. *Science*, *334*(6063), 1664–1664. https://doi.org/10.1126/science.1213357

Schieber, M. H. (2001). Constraints on Somatotopic Organization in the Primary Motor Cortex. *Journal of Neurophysiology*, *86*(5), 2125–2143. https://doi.org/10.1152/jn.2001.86.5.2125

Schleger, F., Landerl, K., Muenssinger, J., Draganova, R., Reinl, M., Kiefer-Schmidt, I., Weiss, M., Wacker-Gußmann, A., Huotilainen, M., & Preissl, H. (2014). Magnetoencephalographic signatures of numerosity discrimination in fetuses and neonates. *Dev Neuropsychol*, *39*(4), 316–329. PubMed. https://doi.org/10.1080/87565641.2014.914212

Schlichting, N., de Jong, R., & van Rijn, H. (2020). Performance-informed EEG analysis reveals mixed evidence for EEG signatures unique to the processing of time. *Psychological Research*, *84*(2), 352–369. https://doi.org/10.1007/s00426-018-1039-y

Schneider, M., Beeres, K., Coban, L., Merz, S., Schmidt, S. S., Stricker, J., & De Smedt, B. (2017). Associations of non-symbolic and symbolic numerical magnitude processing with mathematical competence: A meta-analysis. *Developmental Science*, *20*(3), e12372. https://doi.org/10.1111/desc.12372

Schönbrodt, F. D., Wagenmakers, E.-J., Zehetleitner, M., & Perugini, M. (2017). Sequential hypothesis testing with Bayes factors: Efficiently testing mean differences. *Psychological Methods*, *22*(2), 322–339. https://doi.org/10.1037/met0000061

Schwenk, C., Sasanguie, D., Kuhn, J.-T., Kempe, S., Doebler, P., & Holling, H. (2017). (Non-)symbolic magnitude processing in children with mathematical difficulties: A meta-analysis. *Research in Developmental Disabilities*, *64*, 152–167. https://doi.org/10.1016/j.ridd.2017.03.003

Schwiedrzik, C. M., Bernstein, B., & Melloni, L. (2016). Motion along the mental number line reveals shared representations for numerosity and space. *ELife*, *5*, e10806. https://doi.org/10.7554/eLife.10806

Sengupta, R., Bapiraju, S., & Melcher, D. (2017). Big and small numbers: Empirical support for a single, flexible mechanism for numerosity perception. *Attention, Perception, & Psychophysics*, *79*(1), 253–266. https://doi.org/10.3758/s13414-016-1221-5

Shima, S., Murai, Y., Hashimoto, Y., & Yotsumoto, Y. (2016). Duration Adaptation Occurs Across the Sub- and Supra-Second Systems. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.00114

Shuman, M., & Kanwisher, N. (2004). Numerical Magnitude in the Human Parietal Lobe: Tests of Representational Generality and Domain Specificity. *Neuron*, *44*(3), 557–569. https://doi.org/10.1016/j.neuron.2004.10.008

Simon, O., Kherif, F., Flandin, G., Poline, J.-B., Rivière, D., Mangin, J.-F., Le Bihan, D., & Dehaene, S. (2004). Automatized clustering and functional geometry of human parietofrontal networks for language, space, and number. *NeuroImage*, *23*(3), 1192–1202. https://doi.org/10.1016/j.neuroimage.2004.09.023

Skagerlund, K., Karlsson, T., & Träff, U. (2016). Magnitude Processing in the Brain: An fMRI Study of Time, Space, and Numerosity as a Shared Cortical System. *Frontiers in Human Neuroscience*, *10*. https://doi.org/10.3389/fnhum.2016.00500

Skagerlund, K., & Träff, U. (2014). Development of magnitude processing in children with developmental dyscalculia: Space, time, and number. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.00675

Smeets, J. B. J., & Brenner, E. (2008). Grasping Weber's law. *Current Biology*, *18*(23), R1089–R1090. https://doi.org/10.1016/j.cub.2008.10.008

Sokolowski, H. M., Fias, W., Bosah Ononye, C., & Ansari, D. (2017). Are numbers grounded in a general magnitude processing system? A functional neuroimaging meta-analysis. *Neuropsychologia*, *105*, 50–69. https://doi.org/10.1016/j.neuropsychologia.2017.01.019

Srinivasan, M., & Carey, S. (2010). The long and the short of it: On the nature and origin of functional overlap between representations of space and time. *Cognition*, *116*(2), 217–241. https://doi.org/10.1016/j.cognition.2010.05.005

Stocker, A. A., & Simoncelli, E. (2006). Sensory Adaptation within a Bayesian Framework for Perception. In Y. Weiss, B. Schölkopf, & J. Platt (Eds.), *Advances in Neural Information Processing Systems* (Vol. 18). MIT Press. https://proceedings.neurips.cc/paper/2005/file/c68c9c8258ea7d85472dd6fd0015f047-Paper.pdf

Sun, H.-C., Kingdom, F. A. A., & Baker, C. L. (2017). Texture density adaptation can be bidirectional. *Journal of Vision*, *17*(8), 9. https://doi.org/10.1167/17.8.9

Szkudlarek, E., & Brannon, E. M. (2017). Does the Approximate Number System Serve as a Foundation for Symbolic Mathematics? *Language Learning and Development*, *13*(2), 171–190. https://doi.org/10.1080/15475441.2016.1263573

Takayama, Y., Sugishita, M., Akiguchi, I., & Kimura, J. (1994). Isolated Acalculia due to Left Parietal Lesion. *Archives of Neurology*, *51*(3), 286–291. https://doi.org/10.1001/archneur.1994.00540150084021

Testolin, A., Dolfi, S., Rochus, M., & Zorzi, M. (2020). Visual sense of number vs. Sense of magnitude in humans and machines. *Scientific Reports*, *10*(1), 10045. https://doi.org/10.1038/s41598-020-66838-5

Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology*, *19*(1), R11–R14. https://doi.org/10.1016/j.cub.2008.10.014

Thompson, R. F., Mayers, K. S., Robertson, R. T., & Patterson, C. J. (1970). Number Coding in Association Cortex of the Cat. *Science*, *168*(3928), 271. https://doi.org/10.1126/science.168.3928.271

Tibber, M. S., Greenwood, J. A., & Dakin, S. C. (2012). Number and density discrimination rely on a common metric: Similar psychophysical effects of size, contrast, and divided attention. *Journal of Vision*, *12*(6), 8–8. https://doi.org/10.1167/12.6.8

Togoli, I., & Arrighi, R. (2021). Evidence for an A-Modal Number Sense: Numerosity Adaptation Generalizes Across Visual, Auditory, and Tactile Stimuli. *Frontiers in Human Neuroscience*, *15*, 448. https://doi.org/10.3389/fnhum.2021.713565

Togoli, I., Marlair, C., Collignon, O., Arrighi, R., & Crollen, V. (2021). Tactile numerosity is coded in external space. *Cortex*, *134*, 43–51. https://doi.org/10.1016/j.cortex.2020.10.008

Tokita, M., & Ishiguchi, A. (2011). Temporal information affects the performance of numerosity discrimination: Behavioral evidence for a shared system for numerosity and temporal processing. *Psychonomic Bulletin & Review*, *18*(3), 550–556. https://doi.org/10.3758/s13423-011-0072-2

Tokita, M., & Ishiguchi, A. (2016). Precision and bias in approximate numerical judgment in auditory, tactile, and cross-modal presentation. *Perception*, *45*(1–2), 56–70. https://doi.org/10.1177/0301006615596888

Tolhurst, D. J., Thompson, I. D., & Campbell, F. W. (1981). On the variety of spatial frequency selectivities shown by neurons in area 17 of the cat. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, *213*(1191), 183–199. https://doi.org/10.1098/rspb.1981.0061

Tolias, A. S., Keliris, G. A., Smirnakis, S. M., & Logothetis, N. K. (2005). Neurons in macaque area V4 acquire directional tuning after adaptation to motion stimuli. *Nature Neuroscience*, *8*(5), 591–593. https://doi.org/10.1038/nn1446

Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the "internal clock". *Psychological Monographs: General and Applied*, *77*(13), 1–31. https://doi.org/10.1037/h0093864

Treisman, M., Faulkner, A., Naish, P. L. N., & Brogan, D. (1990). The Internal Clock: Evidence for a Temporal Oscillator Underlying Time Perception with Some Estimates of its Characteristic Frequency. *Perception*, *19*(6), 705–742. https://doi.org/10.1068/p190705

Tsouli, A., Cai, Y., van Ackooij, M., Hofstetter, S., Harvey, B. M., te Pas, S. F., van der Smagt, M. J., & Dumoulin, S. O. (2021). Adaptation to visual numerosity changes neural numerosity selectivity. *NeuroImage*, *229*, 117794. https://doi.org/10.1016/j.neuroimage.2021.117794

Tsouli, A., Dumoulin, S. O., te Pas, S. F., & van der Smagt, M. J. (2019). Adaptation reveals unbalanced interaction between numerosity and time. *Cortex*, *114*, 5–16. https://doi.org/10.1016/j.cortex.2018.02.013

Tsouli, A., van der Smagt, M. J., Dumoulin, S. O., & Te Pas, S. F. (2019). Distinct temporal mechanisms modulate numerosity perception. *Journal of Vision*, *19*(6), 19. https://doi.org/10.1167/19.6.19

Tudusciuc, O., & Nieder, A. (2007). Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. *Proceedings of the National Academy of Sciences*, *104*(36), 14513–14518. https://doi.org/10.1073/pnas.0705495104

Tudusciuc, O., & Nieder, A. (2009). Contributions of Primate Prefrontal and Posterior Parietal Cortices to Length and Numerosity Representation. *Journal of Neurophysiology*, *101*(6), 2984–2994. https://doi.org/10.1152/jn.90713.2008

Tudusciuc, O., & Nieder, A. (2010). Comparison of length judgments and the Müller-Lyer illusion in monkeys and humans. *Experimental Brain Research*, *207*(3), 221–231. https://doi.org/10.1007/s00221-010-2452-7

Turi, M., Burr, D., Igliozzi, R., Aagten-Murphy, D., Muratori, F., & Pellicano, E. (2015). Children with autism spectrum disorder show reduced adaptation to number. *Proceedings of the National Academy of Sciences*, *112*(25), 7868–7872. https://doi.org/10.1073/pnas.1504099112

van den Berg, R., Lindskog, M., Poom, L., & Winman, A. (2017). Recent is more: A negative time-order effect in nonsymbolic numerical judgment. *Journal of Experimental Psychology: Human Perception and Performance*, *43*(6), 1084–1097. https://doi.org/10.1037/xhp0000387

van Dijk, J. A., Fracasso, A., Petridou, N., & Dumoulin, S. O. (2021). Laminar processing of numerosity supports a canonical cortical microcircuit in human parietal cortex. *Current Biology*. https://doi.org/10.1016/j.cub.2021.07.082

van Erp, J. B. F., & Werkhoven, P. J. (2004). Vibro-Tactile and Visual Asynchronies: Sensitivity and Consistency. *Perception*, *33*(1), 103–111. https://doi.org/10.1068/p5014

van Oeffelen, M. P., & Vos, P. G. (1982). A probabilistic model for the discrimination of visual number. *Perception & Psychophysics*, *32*(2), 163–170. https://doi.org/10.3758/BF03204275

VanMarle, K., & Wynn, K. (2006). Six-month-old infants use analog magnitudes to represent duration. *Developmental Science*, *9*(5), F41–F49. https://doi.org/10.1111/j.1467-7687.2006.00508.x

Vetter, P., Butterworth, B., & Bahrami, B. (2008). Modulating Attentional Load Affects Numerosity Estimation: Evidence against a Pre-Attentive Subitizing Mechanism. *PLOS ONE*, *3*(9), e3269. https://doi.org/10.1371/journal.pone.0003269

Vicario, C. M., Rappo, G., Pepi, A., Pavan, A., & Martino, D. (2012). Temporal Abnormalities in Children With Developmental Dyscalculia. *Developmental Neuropsychology*, *37*(7), 636–652. https://doi.org/10.1080/87565641.2012.702827

Viswanathan, P., & Nieder, A. (2013). Neuronal correlates of a visual "sense of number" in primate parietal and prefrontal cortices. *Proceedings of the National Academy of Sciences*, *110*(27), 11187–11192. https://doi.org/10.1073/pnas.1308141110

Wade, N., & Verstraten, F. (2005). Accommodating the past: A selective history of adaptation. In C. W. G. Clifford & G. Rhodes (Eds.), *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision* (pp. 83--101). Oxford University Press.

Wagener, L., Loconsole, M., Ditz, H. M., & Nieder, A. (2018). Neurons in the Endbrain of Numerically Naive Crows Spontaneously Encode Visual Numerosity. *Current Biology*, *28*(7), 1090-1094.e4. https://doi.org/10.1016/j.cub.2018.02.023

Wagenmakers, E.-J. (2007). A practical solution to the pervasive problems ofp values. *Psychonomic Bulletin & Review*, *14*(5), 779–804. https://doi.org/10.3758/BF03194105

Walker, J. T., Irion, A. L., & Gordon, D. G. (1981). Simple and contingent aftereffects of perceived duration in vision and audition. *Perception & Psychophysics*, *29*(5), 475–486. https://doi.org/10.3758/BF03207361

Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*(11), 483–488. https://doi.org/10.1016/j.tics.2003.09.002

Wandell, B. A., Dumoulin, S. O., & Brewer, A. A. (2007). Visual Field Maps in Human Cortex. *Neuron*, *56*(2), 366–383. https://doi.org/10.1016/j.neuron.2007.10.012

Wandell, B. A., & Winawer, J. (2015). Computational neuroimaging and population receptive fields. *Trends in Cognitive Sciences*, *19*(6), 349–357. https://doi.org/10.1016/j.tics.2015.03.009

Warrington, E. K. (1982). The Fractionation of Arithmetical Skills: A Single Case Study. *The Quarterly Journal of Experimental Psychology Section A*, *34*(1), 31–51. https://doi.org/10.1080/14640748208400856

Wearden, J. H., & Bray, S. (2001). Scalar Timing without Reference Memory? Episodic Temporal Generalization and Bisection in Humans. *The Quarterly Journal of Experimental Psychology Section B*, *54*(4b), 289–309. https://doi.org/10.1080/713932763

Wearden, J. H., & Lejeune, H. (2008). Scalar Properties in Human Timing: Conformity and Violations. *Quarterly Journal of Experimental Psychology*, *61*(4), 569–587. https://doi.org/10.1080/17470210701282576

Weber, E. H. (1834). *De pulsu, resorptione, auditu et tactu: Annotationes anatomicae et physiologicae, auctore*. prostat apud CF Koehler.

Webster, M. A. (2011). Adaptation and visual coding. *Journal of Vision*, *11*(5), 3–3. https://doi.org/10.1167/11.5.3

Webster, M. A. (2012). Evolving concepts of sensory adaptation. *F1000 Biology Reports*, *4*, 21. https://doi.org/10.3410/B4-21

Webster, M. A. (2015). Visual Adaptation. *Annual Review of Vision Science*, *1*(1), 547–567. https://doi.org/10.1146/annurev-vision-082114-035509

Whalen, J., Gallistel, C. R., & Gelman, R. (1999). Nonverbal Counting in Humans: The Psychophysics of Number Representation. *Psychological Science*, *10*(2), 130–137. https://doi.org/10.1111/1467-9280.00120

Wohlgemuth, A. (1911). *On the after-effect of seen movement* (Issues 1–2). University Press.

Wright, B. A., Buonomano, D. V., Mahncke, H. W., & Merzenich, M. M. (1997). Learning and Generalization of Auditory Temporal–Interval Discrimination in Humans. *The Journal of Neuroscience*, *17*(10), 3956. https://doi.org/10.1523/JNEUROSCI.17-10-03956.1997

Xu, F. (2003). Numerosity discrimination in infants: Evidence for two systems of representations. *Cognition*, *89*(1), B15–B25. https://doi.org/10.1016/S0010-0277(03)00050-7

Xu, F., & Arriaga, R. I. (2007). Number discrimination in 10-month-old infants. *British Journal of Developmental Psychology*, *25*(1), 103–108. https://doi.org/10.1348/026151005X90704

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition*, *74*(1), B1–B11. https://doi.org/10.1016/S0010-0277(99)00066-9

Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision*, *7*(10), 2. https://doi.org/10.1167/7.10.2

Young, E. D. (1998). Parallel processing in the nervous system: Evidence from sensory maps. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(3), 933–934. PubMed. https://doi.org/10.1073/pnas.95.3.933

Zimmermann, E., & Fink, G. R. (2016). Numerosity perception after size adaptation. *Scientific Reports*, *6*(1), 32810. https://doi.org/10.1038/srep32810

Zorzi, M., & Testolin, A. (2018). An emergentist perspective on the origin of number sense. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1740), 20170043. https://doi.org/10.1098/rstb.2017.0043

Appendix

Supplementary materials

Chapter 2

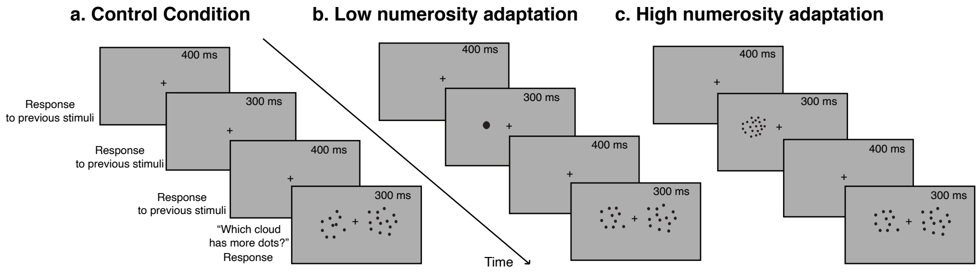
Stimulus validation

Apparatus and Stimuli

We tested 10 participants, 6 of whom had also participated in the fMRI experiment. Participants were tested on a MacBook Pro and sat at about 60 cm distance from the display (display dimensions: 32 × 29 cm, resolution: 1280 × 800, refresh rate: 60 Hz). In the adaptation conditions, the adapters were circular patches of 1 dot (diameter: 0.6˚ of visual angle) or 20 dots (diameter: 0.15˚ of visual angle), while the reference stimulus was a patch of 10 dots (diameter: 0.2˚ of visual angle). The circular patches had a diameter of 7˚. In each trial, dots were scattered randomly within the circular patches and were not allowed to overlap. The center of the dot patches was at 8˚ eccentricity left of fixation for the first half of the trials and right of fixation for the other half (100 trials in total). All stimuli were generated and presented using MATLAB 2016b (MathWorks, Inc.) and the Psychophysics Toolbox 3.0.13 (Brainard, 1997; Pelli, 1997).

Procedure

In the control condition, no adapter stimulus was shown (S1a). In the adaptation conditions, the adapter was shown for 300 ms, followed by an interstimulus interval of 400 ms. The reference patch was then presented for 300 ms at the same location as the adapter, and the test patch appeared at the opposite side of fixation (S1b,c). The numerosity of the test patch varied from trial to trial using the Minimum Expected Entropy staircase method[1]. When half of the trials were completed, the adapter and reference stimuli would appear on the opposite side of the fixation (i.e. on the right side, if during the first half of the trials they were presented on the left).



S1. *Schematic representation of stimuli presentation in each condition.* In the control condition, no adapter was presented. In the low and high numerosity adaptation conditions, the adapter was 1 and 20 dots respectively (similarly to our fMRI paradigm), and we tested the effect of their presentation on a reference stimulus of 10 dots appearing in the same location. The test stimulus

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[1] Saunders, J. A., & Backus, B. T. (2006). Perception of surface slant from oriented textures. *Journal of Vision, 6*(9), 882e897. https://doi.org/10.1167/6.9.3.

was presented in the opposite side and varied in numerosity using a staircase method. Participants were asked to respond which of the two patches (the reference or the test) contained more dots. In an effort to stay as close as possible to our fMRI paradigm, the trial sequence was not interrupted "waiting" for the participant to respond, and if the participant failed to respond within a certain time window, the same trial would be repeated.

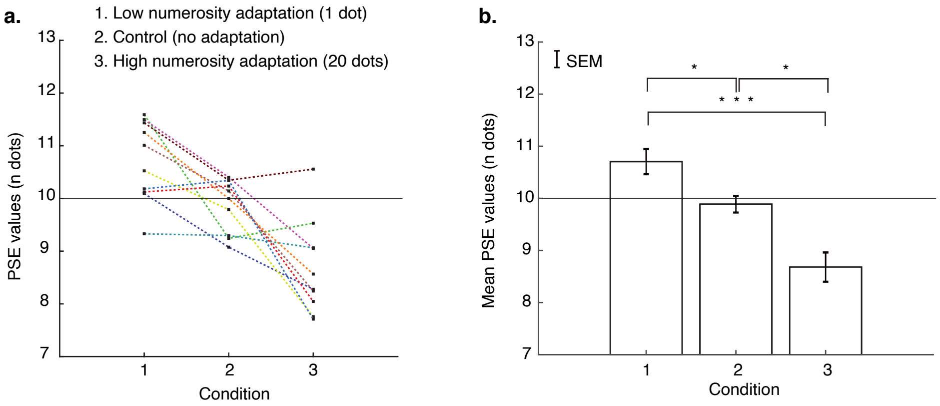
Our choice of presenting the adapter and reference stimulus on one side and the test stimulus on the opposite side was based on findings suggesting that adaptation to numerosity is spatially specific (Aagten-Murphy & Burr, 2016; Arrighi et al., 2014; Burr & Ross, 2008).

Participants were instructed to maintain fixation at the central cross throughout the experiment. Then, using the two-alternative forced-choice (2AFC) paradigm, participants were asked to respond as fast and accurately as possible (guessing if unsure) which of the two patches, the reference or the test, appeared to have more dots by pressing the appropriate key. Given that we wanted to translate as closely as possible our fMRI paradigm to the behavioral task, we used the same presentation durations and interstimulus intervals as in our fMRI adaptation paradigm. Moreover, the trial sequence in the behavioral task was not interrupted by "waiting" for the participant to give a response. Instead, and as shown in figure S1, the participant was allowed to respond at any time point before the new reference and test stimuli appeared, and if the participant failed to do so, the same trial would be repeated.

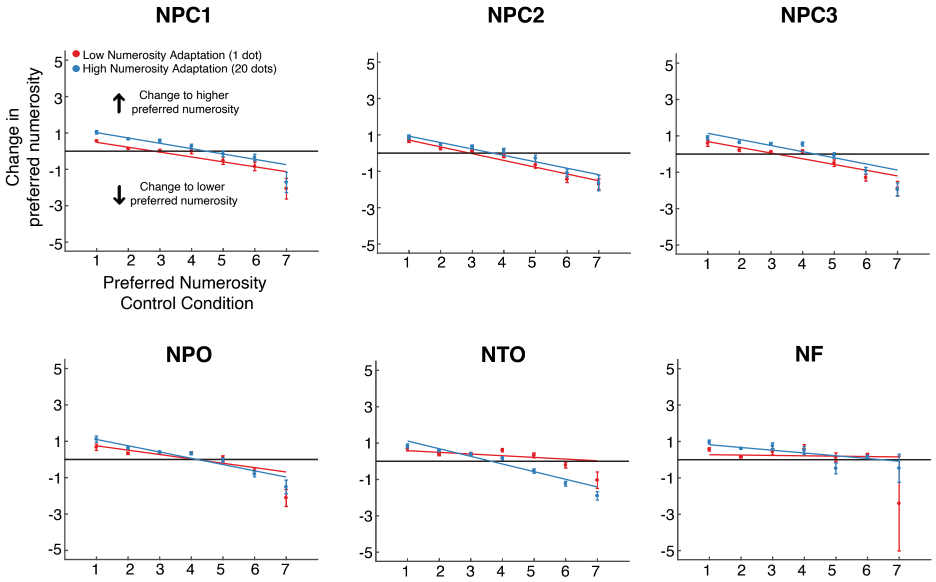
After the experiment, we ordered the data by adding the values obtained per presentation side (left vs. right of the fixation cross), sorting them on test numerosity and subsequently creating 10 equally sized bins of 10 trials. We then fitted these data with cumulative Gaussian functions to yield estimates of the point of subjective equality (PSE) for each condition which we used to quantify the effect of numerosity adaptation on numerosity perception.

Results

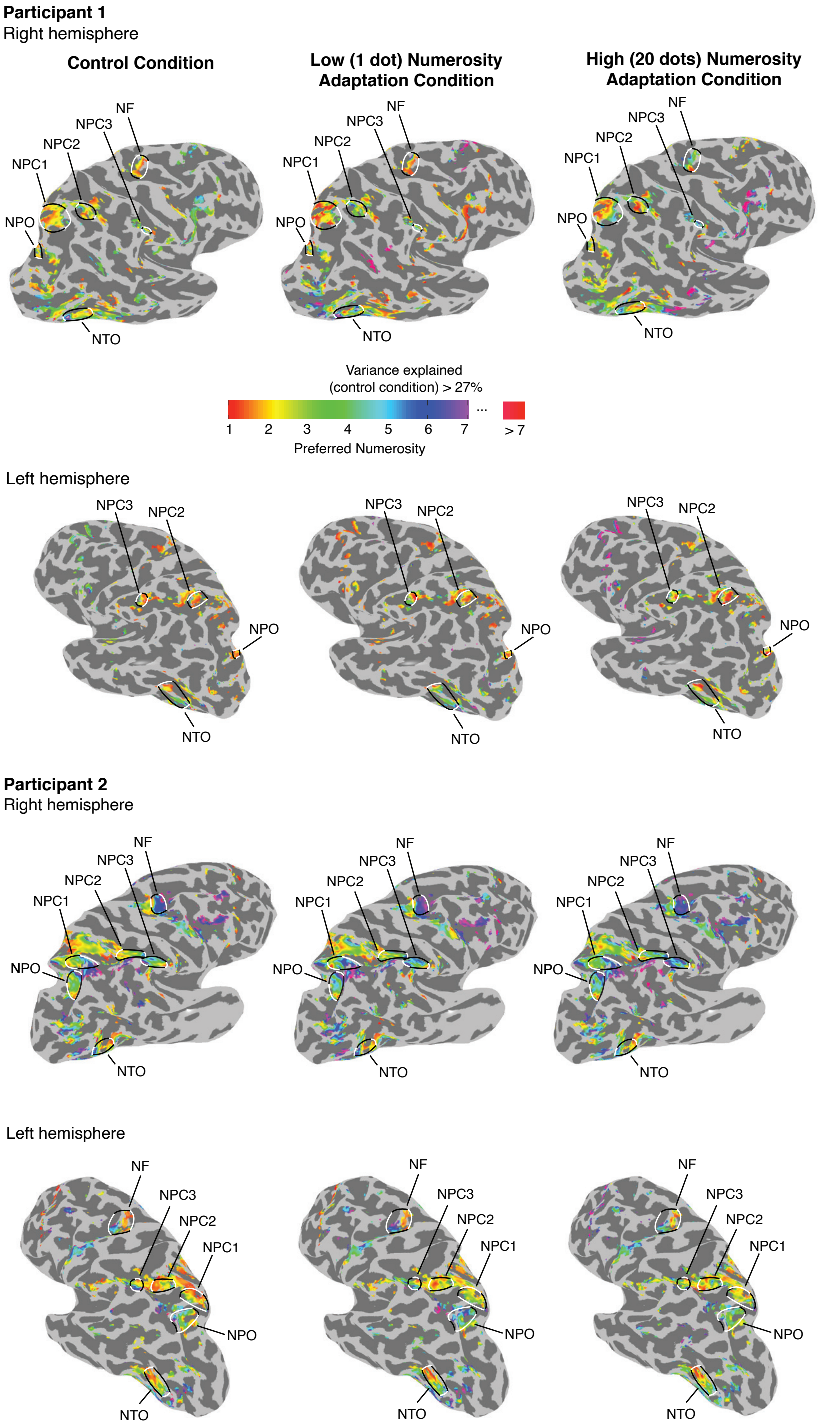
We performed a one-way repeated-measures ANOVA after ensuring that the data was normally distributed (Shapiro-Wilk test, $p > 0.05$) and the sphericity assumption was not violated (Mauchly's test, $\chi^2(2) = 1.215$, $p > 0.05$). There was a significant main effect of adaptation condition on PSE values (F (2, 18) = 26.48, $p < 0.001$, partial $\eta^2 = .75$). As illustrated in figure S2, pair-wise comparisons with Bonferroni correction showed that participants had significantly higher PSE values after adaptation to a low numerosity adapter (Mean = 10.70, $SD = 0.24$) compared to the control condition (Mean = 9.89, $SD = 0.16$; $p = 0.023$), and when compared to adaptation to a high numerosity adapter (Mean = 8.68, $SD = 0.28$; $p < 0.001$). The PSE values after high numerosity adaptation were significantly lower compared to the control condition ($p = 0.015$). These results provide behavioral evidence for perceptual repulsion in accordance with numerosity adaptation even when using a fast adaptation protocol like the one used in our fMRI experiment.

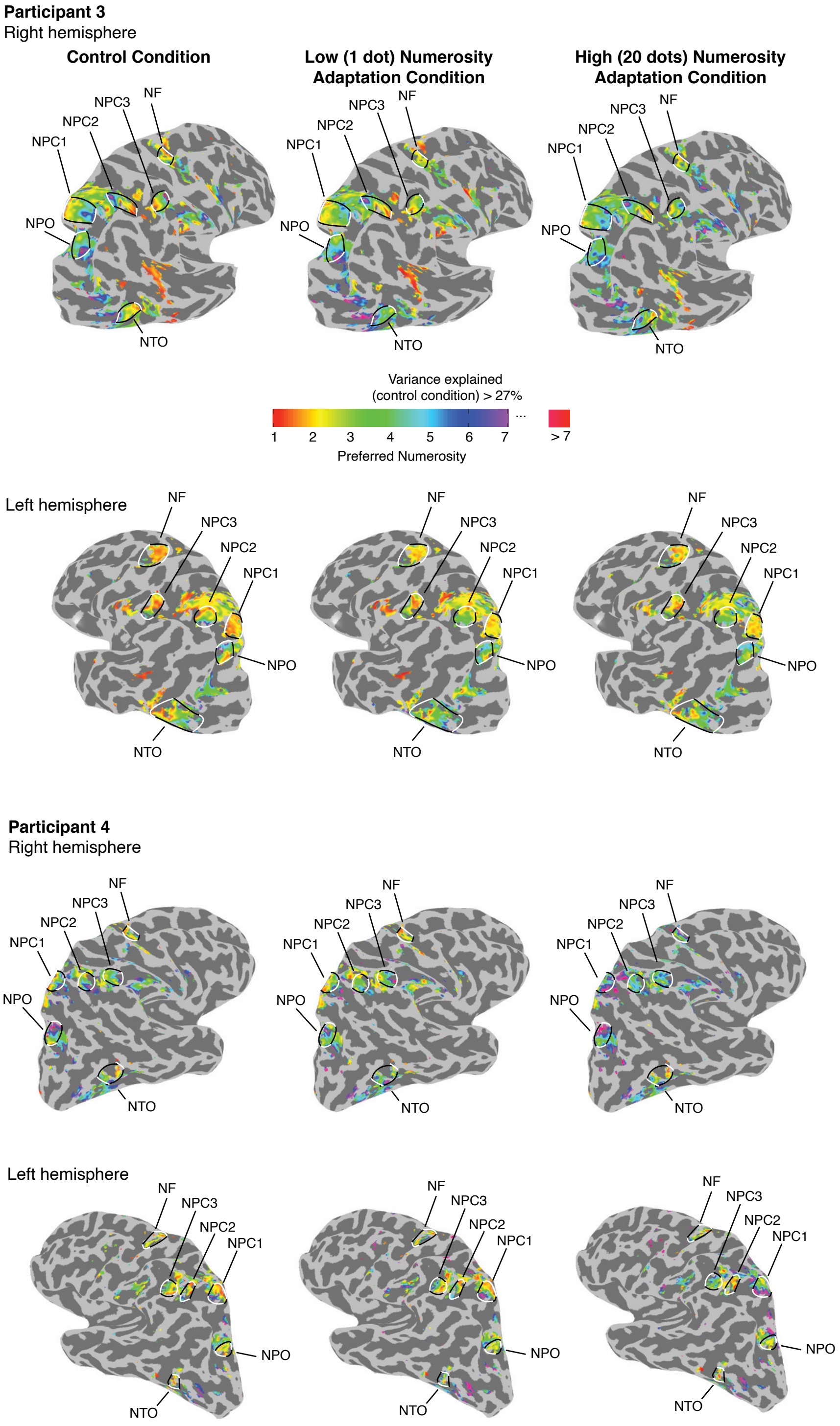


S2. *PSE values per participant (N=10) and on a group-level for each condition.* (a) In most participants, and compared to the control condition, the perception of the reference stimulus was repelled from the numerosity of the adapter, with an increase in the perceived numerosity (i.e. higher PSE values) of the reference stimulus (10 dots) after low numerosity adaptation, and a decrease in the perceived numerosity (i.e. lower PSE values) after high numerosity adaptation. (b) These changes in perceived numerosity of the reference stimulus after low and high numerosity adaptation are further illustrated on a group level, where each condition was significantly different from both others (*p ≤ 0.05, ***p ≤ 0.001, Bonferroni-corrected).

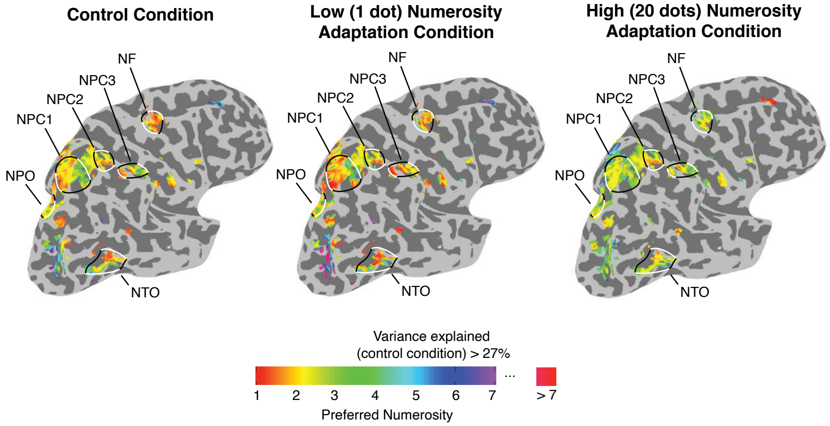


S3. *Change in preferred numerosity after low (in red) and high (in blue) numerosity adaptation as a function of the unadapted preferred numerosity (control condition).* Each point represents the mean preferred numerosity in each numerosity bin and error bars correspond to the standard error of the mean (SEM). Positive and negative values on the y axis represent a change of preferred numerosities towards higher and lower preferred numerosities respectively. In both adaptation conditions, the preferences of recording sites with lower preferred numerosities in the control condition, changed to higher preferred numerosities, whereas the preferences of recording sites with higher preferred numerosities in the control condition, changed to lower preferred numerosities. The linear fits shown are not identical between the two adaptation conditions, suggesting a distinct effect of each adapter.

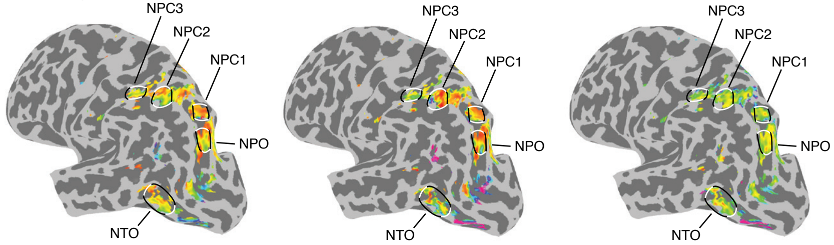

Participant 1
Right hemisphere
Control Condition
Low (1 dot) Numerosity Adaptation Condition
High (20 dots) Numerosity Adaptation Condition
NF
NPC3
NPC2
NPC1
NPO
NTO
Variance explained (control condition) > 27%
1
2
3
4
5
6
7
...
> 7
Preferred Numerosity
Left hemisphere
NPC3
NPC2
NPO
NTO
Participant 2
Right hemisphere
NF
NPC3
NPC2
NPC1
NPO
NTO
Left hemisphere
NF
NPC3
NPC2
NPC1
NPO
NTO


Participant 3
Right hemisphere
Control Condition
Low (1 dot) Numerosity Adaptation Condition
High (20 dots) Numerosity Adaptation Condition
NF
NPC3
NPC2
NPC1
NPO
NTO
NF
NPC3
NPC2
NPC1
NPO
NTO
NF
NPC3
NPC2
NPC1
NPO
NTO
Variance explained (control condition) > 27%
1
2
3
4
5
6
7
...
> 7
Preferred Numerosity
Left hemisphere
NF
NPC3
NPC2
NPC1
NPO
NTO
NF
NPC3
NPC2
NPC1
NPO
NTO
NF
NPC3
NPC2
NPC1
NPO
NTO
Participant 4
Right hemisphere
NF
NPC3
NPC2
NPC1
NPO
NTO
NF
NPC3
NPC2
NPC1
NPO
NTO
NF
NPC3
NPC2
NPC1
NPO
NTO
Left hemisphere
NF
NPC3
NPC2
NPC1
NPO
NTO
NF
NPC3
NPC2
NPC1
NPO
NTO
NF
NPC3
NPC2
NPC1
NPO
NTO

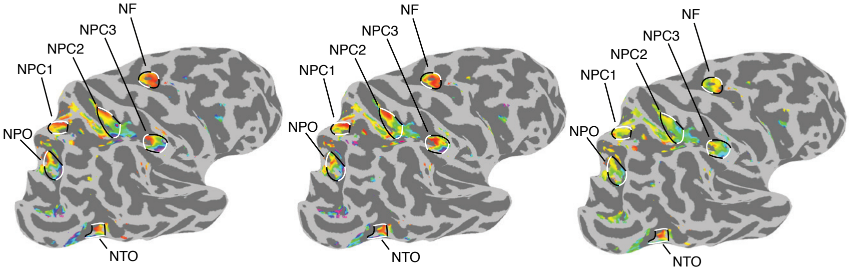
Participant 5
Right hemisphere



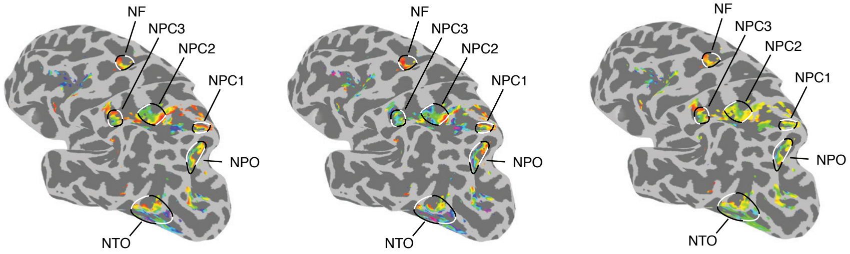
Left hemisphere



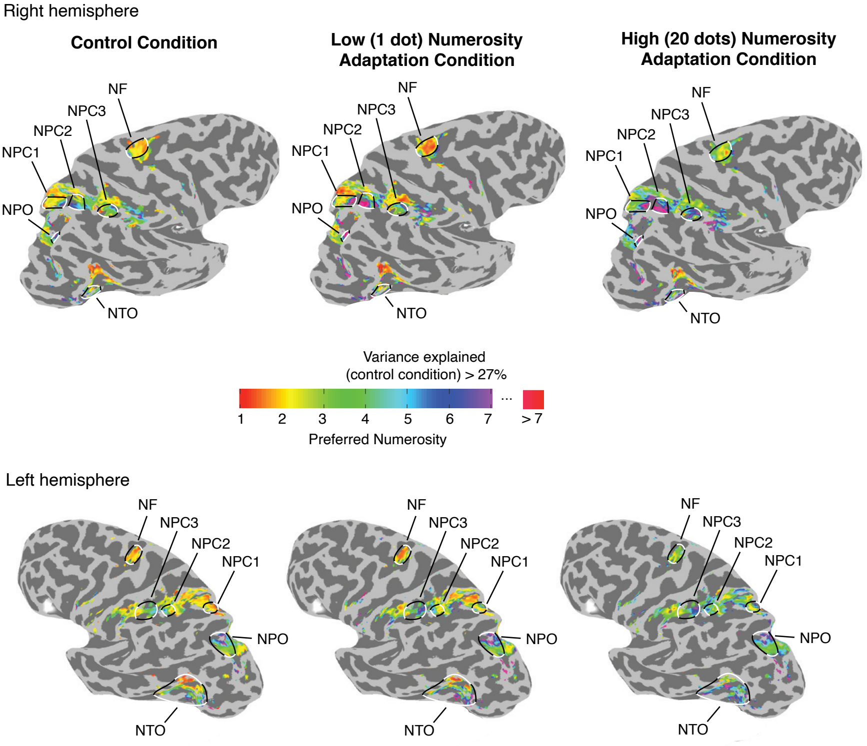
Participant 6
Right hemisphere



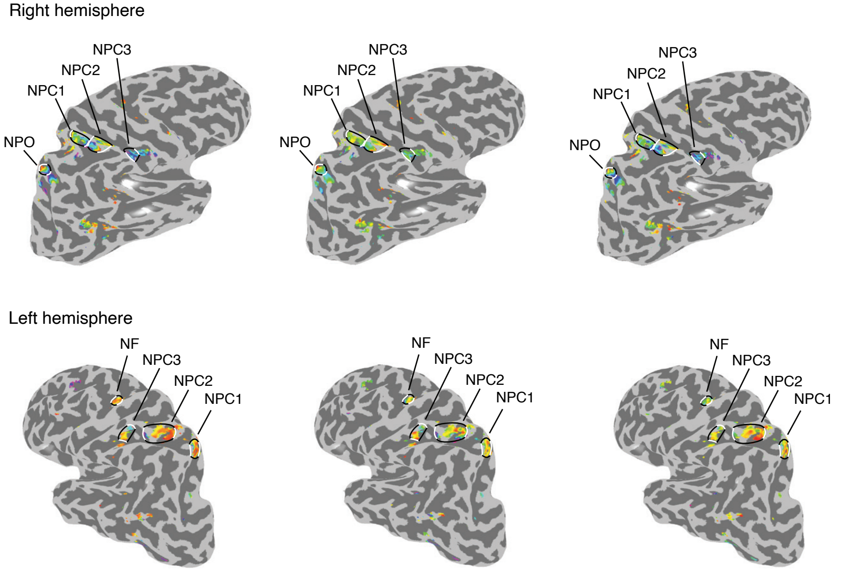
Left hemisphere



Participant 7



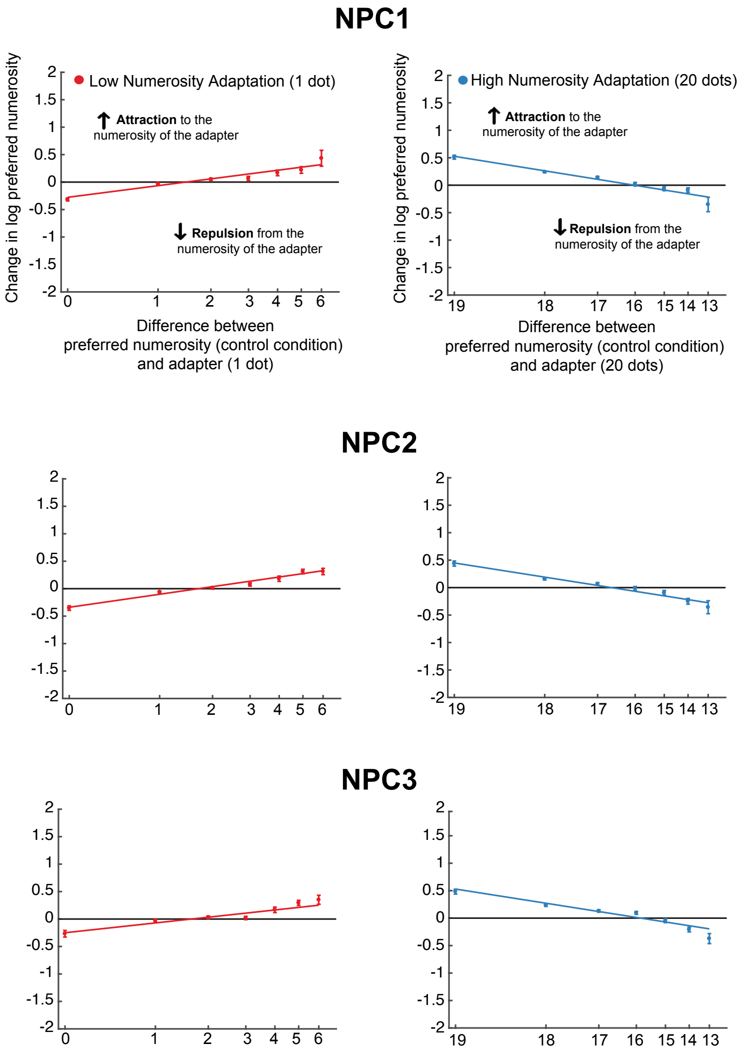
Participant 8

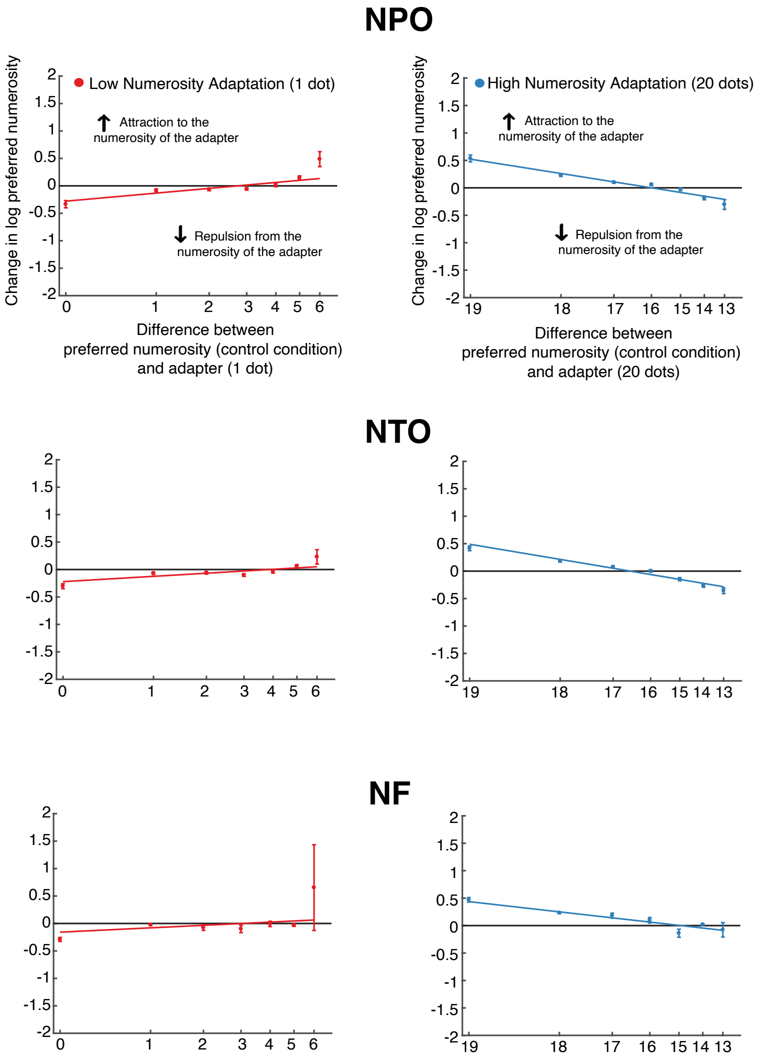


S4. *Numerosity selective areas in each hemisphere of each participant.* We found six topographic numerosity maps, i.e. extended areas where preferred numerosity changed gradually across the cortical surface. Colors show each recording site's preferred numerosity. White lines mark the borders of recording sites with the highest or lowest preferred numerosity present in each numerosity map. Black lines show borders of numerosity maps. Compared to the control condition, preferred numerosities within the numerosity maps were overall lower after low numerosity adaptation, and higher after high numerosity adaptation.

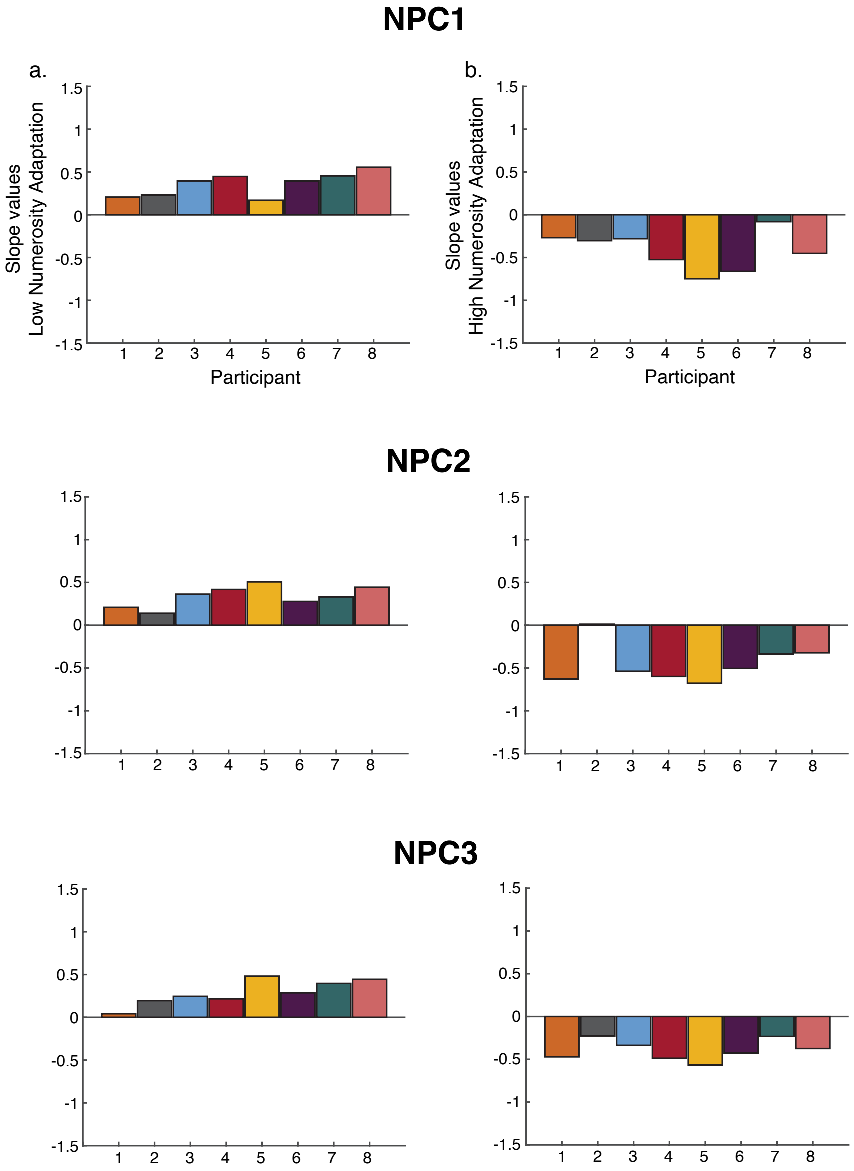
Table 1. *Numerosity selective areas identified in the right (RH) and left (LH) hemisphere of each participant. The instances where these areas were not identifiable are marked with* ×.

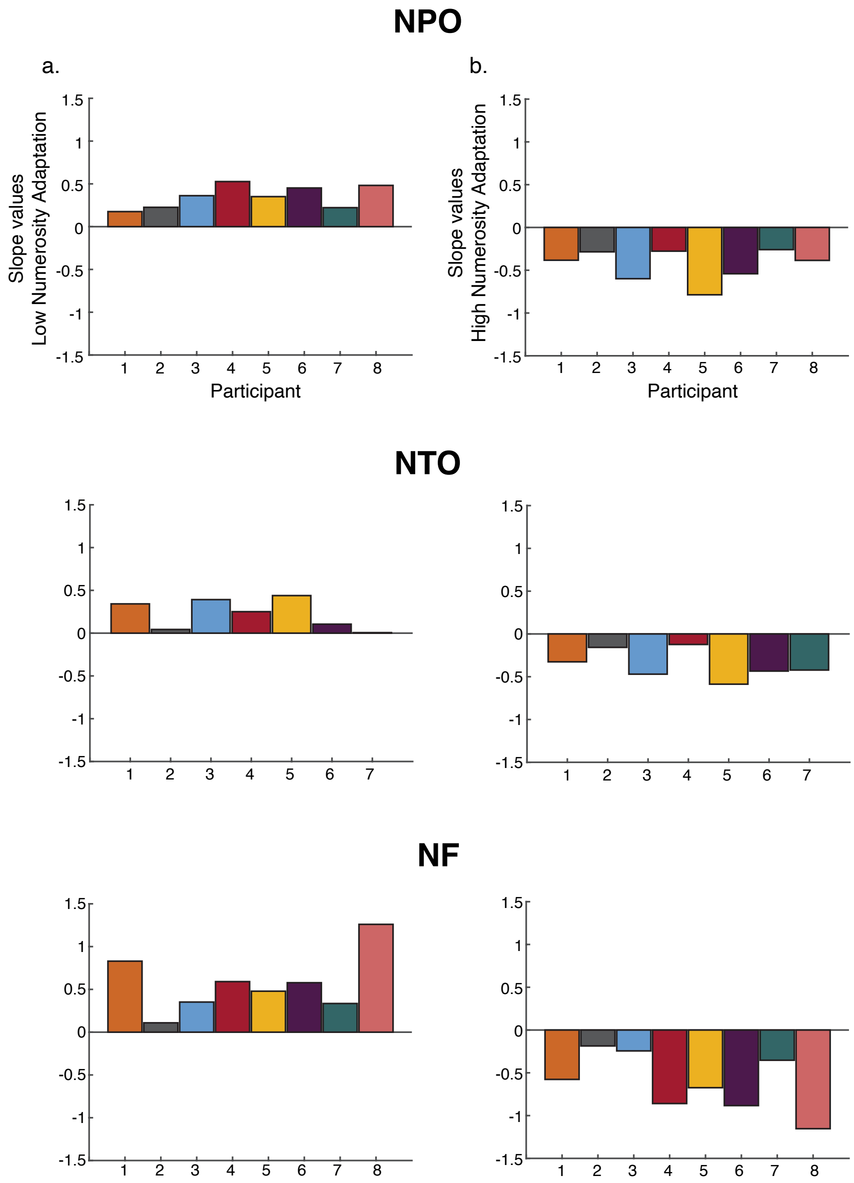
	Numerosity selective areas											
	NPC1		NPC2		NPC3		NPO		NTO		NF	
Participant	RH	LH	RH	LH	RH	LH	RH	LH	RH	LH	RH	LH
1	✓	×	✓	✓	✓	✓	✓	✓	✓	✓	✓	×
2	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
3	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
4	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
5	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	×
6	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
7	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
8	✓	✓	✓	✓	✓	✓	✓	×	×	×	×	✓


NPC1
Low Numerosity Adaptation (1 dot)
High Numerosity Adaptation (20 dots)
Attraction to the numerosity of the adapter
Repulsion from the numerosity of the adapter
Change in log preferred numerosity
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
0 1 2 3 4 5 6
19 18 17 16 15 14 13
Difference between preferred numerosity (control condition) and adapter (1 dot)
Difference between preferred numerosity (control condition) and adapter (20 dots)
NPC2
NPC3



S5. *Change in natural logarithmic preferred numerosity as a function of the difference between the preferred numerosity in the control condition and the numerosity of the adapter on a logarithmic scale.* Each point represents the mean preferred numerosity in each numerosity bin and error bars correspond to the SEM. When the preferred numerosity in the control condition is numerically closer to the numerosity of the adapter, preferred numerosities are repulsed from the numerosity of the adapter in each adaptation condition. However, when the preferred numerosity in the control condition is numerically further from the numerosity of the adapter, preferred numerosities are attracted to the numerosity of the adapter. This trend was evident in all numerosity maps.


NPC1
a.
b.
Slope values
Low Numerosity Adaptation
Slope values
High Numerosity Adaptation
1.5
1
0.5
0
-0.5
-1
-1.5
1
2
3
4
5
6
7
8
Participant
NPC2
NPC3

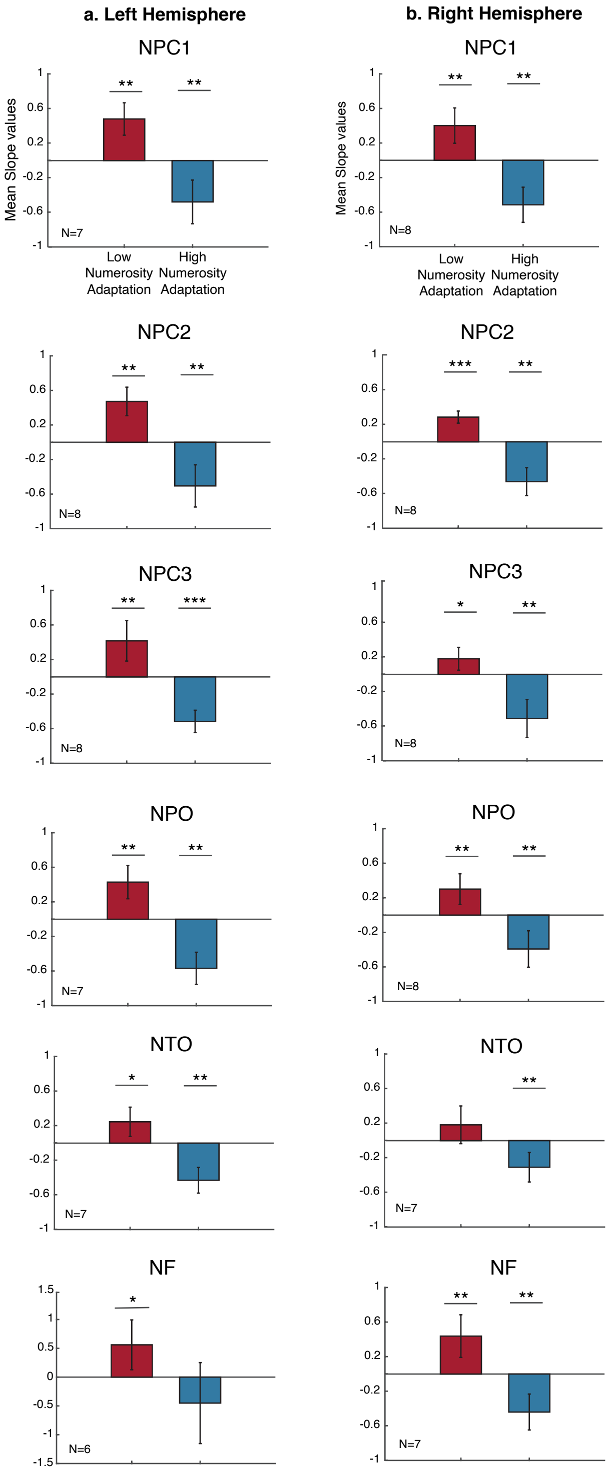


S6. *Slope values of the change in logarithmic preferred numerosity for each participant and numerosity map.* The slope values of each participant for each numerosity map were calculated using a simple linear regression method. (a) We found positive slope values in the low numerosity adaptation condition and (b) negative slope values in the high numerosity adaptation condition in all participants. This finding illustrates further the attraction to the numerosity of the adapter when preferred numerosities are numerically further from the numerosity of the adapter. This trend was evident in all numerosity maps.

We also did a group-level analysis to examine whether the slope values in each adaptation condition and numerosity map were significantly different from zero across participants separately for the left- and right-hemisphere numerosity maps (Figure S7). We conducted a series of one-sample *t*-tests, after ensuring that the normality assumption was not violated by conducting a series of the Shapiro–Wilk tests ($p > 0.05$ for each variable), and used false discovery rate (FDR)-corrected significance thresholds.

In the low numerosity adaptation condition, we found that the slope values were significantly different from zero and this difference was statistically significant in almost all numerosity maps in both the left- and right-hemisphere ($NPC1_{LH}$: Mean = 0.48, SE = 0.08, $t(6) = 6.28$, $p = 0.002$; $NPC1_{RH}$: Mean = 0.40, SE = 0.09, $t(7) = 4.65$, $p = 0.004$; $NPC2_{LH}$: Mean = 0.47, SE = 0.07, $t(7) = 6.77$, $p = 0.0014$; $NPC2_{RH}$: Mean = 0.29, SE = 0.03, $t(7) = 9.70$, $p = 0.0004$; $NPC3_{LH}$: Mean = 0.42, SE = 0.10, $t(7) = 4.22$, $p = 0.006$; $NPC3_{RH}$: Mean = 0.18, SE = 0.06, $t(7) = 3.23$, $p = 0.016$; NPO_{LH}: Mean = 0.43, SE = 0.08, $t(6) = 5.47$, $p = 0.004$; NPO_{RH}: Mean = 0.30, SE = 0.08, $t(7) = 4.01$, $p = 0.007$; NTO_{LH}: Mean = 0.25, SE = 0.07, $t(6) = 3.57$, $p = 0.014$; NTO_{RH}: Mean = 0.18, SE = 0.09, $t(6) = 2.06$, $p > 0.05$; NF_{LH}: Mean = 0.56, SE = 0.17, $t(5) = 3.33$, $p = 0.023$; NF_{RH}: Mean = 0.44, SE = 0.10, $t(6) = 4.36$, $p = 0.006$, FDR-corrected significance thresholds).

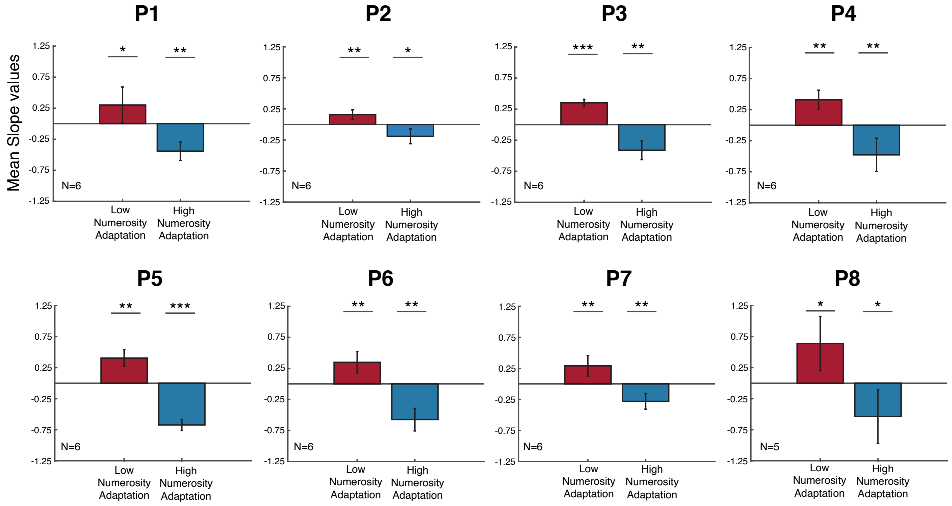
The same pattern was found in the high numerosity adaptation condition where the mean slope values were significantly different from zero and this difference was statistically significant in almost all numerosity maps in both the left- and right-hemisphere ($NPC1_{LH}$: Mean = -0.48, SE = 0.10, $t(6) = -4.63$, $p = 0.006$; $NPC1_{RH}$: Mean = -0.51, SE = 0.09, $t(7) = -5.99$, $p = 0.002$; $NPC2_{LH}$: Mean = -0.51, SE = 0.10, $t(7) = -4.89$, $p = 0.004$; $NPC2_{RH}$: Mean = -0.46, SE = 0.07, $t(7) = -6.76$, $p = 0.0014$; $NPC3_{LH}$: Mean = -0.52, SE = 0.05, $t(7) = -9.42$, $p = 0.0004$; $NPC3_{RH}$: Mean = -0.51, SE = 0.09, $t(7) = -5.51$, $p = 0.002$; NPO_{LH}: Mean = -0.57, SE = 0.08, $t(6) = -7.47$, $p = 0.0014$; NPO_{RH}: Mean = -0.39, SE = 0.09, $t(7) = -4.40$, $p = 0.005$; NTO_{LH}: Mean = -0.43, SE = 0.06, $t(6) = -7.09$, $p = 0.002$; NTO_{RH}: Mean = -0.31, SE = 0.07, $t(6) = -4.42$, $p = 0.006$; NF_{LH}: Mean = -0.45, SE = 0.27, $t(5) = -1.65$, $p > 0.05$; NF_{RH}: Mean = -0.44, SE = 0.09, $t(6) = -5.17$, $p = 0.004$, FDR-corrected significance thresholds).


a. Left Hemisphere
b. Right Hemisphere
NPC1
NPC2
NPC3
NPO
NTO
NF
Mean Slope values
1
0.6
0.2
-0.2
-0.6
-1
1.5
0.5
0
-0.5
-1.5
*
**
***
N=6
N=7
N=8
Low Numerosity Adaptation
High Numerosity Adaptation

S7. *Mean slope values of the change in logarithmic preferred numerosity in each numerosity map and adaptation condition across participants separately for the (a) left- and (b) right-hemisphere numerosity maps.* The error bars correspond to the 95% confidence intervals of the mean slope values, and asterisks denote the level of statistical significance of the one-sample *t*-tests (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, FDR-corrected). N corresponds to the number of participants in which each map was identified. In almost adaptation conditions and left- and right-hemisphere numerosity maps, we found that the mean slope values were statistically different from zero, further validating the finding that preferred numerosity is attracted to the numerosity of the adapter when they are numerically further from each other.

We also examined whether the slope values in each adaptation condition were significantly different from zero across numerosity maps identified in each participant.

As shown in Figure S8, and in the case of low numerosity adaptation condition, the mean slope values were significantly different from zero and this difference was statistically significant in all participants (P1: Mean = 0.30, *SE* = 0.11, *t*(5) = 2.67, p = 0.045; P2: Mean = 0.16, *SE* = 0.03, *t*(5) = 5.23, p = 0.01; P3: Mean = 0.35, *SE* = 0.02, *t*(5) = 15.66, p < 0.001; P4: Mean = 0.41, *SE* = 0.06, *t*(5) = 6.72, p = 0.003; P5: Mean = 0.40, *SE* = 0.05, *t*(5) = 7.76, p = 0.002; P6: Mean = 0.35, *SE* = 0.07, *t*(5)= 5.23, p = 0.005, P7: Mean = 0.29, *SE* = 0.07, *t*(5) = 4.47, p = 0.01, P8: Mean = 0.64, *SE* = 0.16, *t*(4) = 4.06, p = 0.02, FDR-corrected significance thresholds). In the case of high numerosity adaptation condition, the mean slope values were also significantly different from zero and this difference was statistically significant in all participants (P1: Mean = -0.44, *SE* = 0.06, *t*(5) = -7.63, p = 0.002; P2: Mean = -0.19, *SE* = 0.05, *t*(5) = -4.10, p = 0.012; P3: Mean = -0.41, *SE* = 0.06, *t*(5) = -6.94, p = 0.003; P4: Mean= -0.48, *SE* = 0.10, *t*(5) = -4.57, p = 0.01; P5: Mean = -0.67, *SE* = 0.04, *t*(5) = -19.11, p < 0.001; P6: Mean = -0.58, *SE* = 0.07, *t*(5) = -8.12, p = 0.002, P7: Mean = -0.28, *SE* = 0.05, *t*(5) = -5.77, p = 0.004, P8: Mean = -0.54, *SE* = 0.16, *t*(4) = -3.46, p = 0.03, FDR-corrected significance thresholds).



S8. *Mean slope values of the change in logarithmic preferred numerosity in each adaptation condition across the numerosity maps identified in each participant.* The error bars correspond to the 95% confidence intervals of the mean slope values, and asterisks denote the level of statistical significance of the one-sample *t*-tests (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, FDR-corrected). N corresponds to the number of numerosity maps identified in each participant. In all participants and adaptation conditions, we found that the mean slope values were statistically different from zero, further validating the finding that preferred numerosity is attracted to the numerosity of the adapter when they are numerically further from each other.

Chapter 3

Sequential analysis graphs using the JASP software for Bayesian statistics

In order to examine the possibility that increasing our sample size could have yielded a different statistical outcome especially in the case of numerosity adaptation and testing on duration discrimination, we hereby report the sequential analysis plots which show how the Bayes factor develops as the data points accumulate. Compared to the other experimental conditions, and in the case of numerosity adaptation-duration discrimination task (Figure 1c), there is no definitive trend found as the data accumulate, and the evidence for H_1 (PSE values in duration discrimination differ after adaptation to 20 compared to 80 dots) is almost the same as the evidence for H_0 (no difference in PSE values).

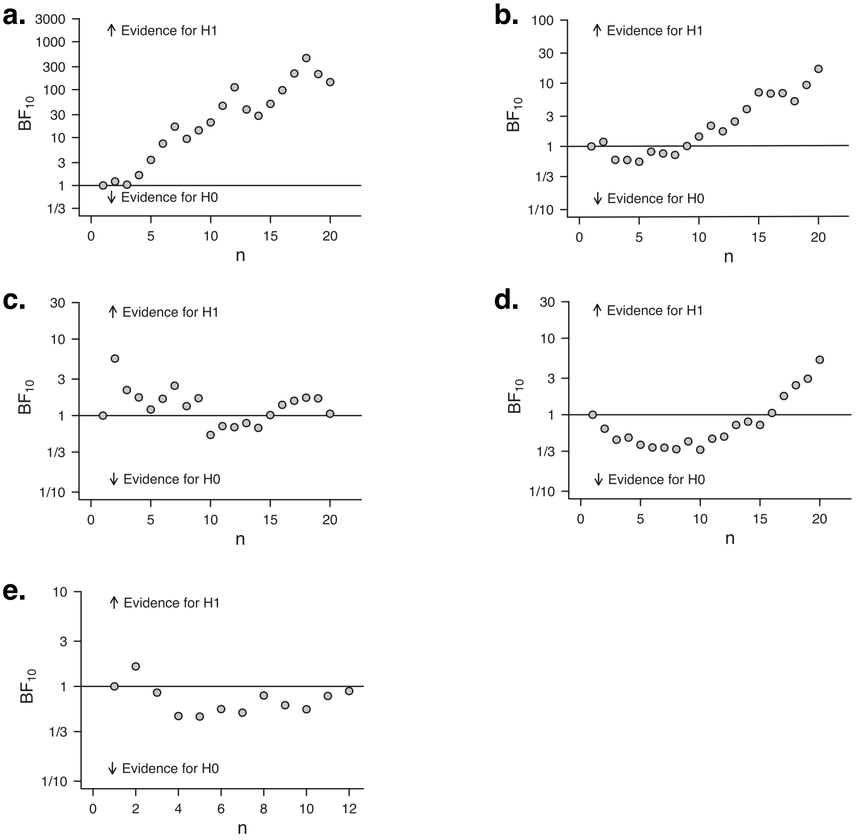


Figure 1. *JASP graphical output for sequential analyses.* (a) In the numerosity adaptation-numerosity discrimination condition, the sequential analysis presented displays the flow of evidence for H_1 (PSE values in numerosity discrimination differ after adaptation to 20 compared to 80 dots) vs. H_0 (no difference in PSE values) as the data accumulate, and shows that the evidence for H_1 (y-axis) increases with the number of data points (x-axis). (b) The same trend is seen in the duration adaptation-duration discrimination condition. (c) In the numerosity adaptation-duration discrimination condition, there is no definitive trend found as the data accumulate, and the evidence for H_1 is almost the same as the evidence for H_0. (d) In the duration adaptation-numerosity discrimination condition, the evidence for H1 increases with the number of data points.

Examining the role of numerosity adapter size on duration processing

To further investigate the role of the size of the RFs of neurons tuned to numerosity and duration processing, we doubled the size of the dot stimuli used as numerosity adapters by moving the monitor closer to the participants at about 30 cm distance (original distance was 60 cm), and retested 12 participants from our original sample on the duration discrimination task.

The mean PSE values in duration discrimination task (Figure 2) were marginally higher after adaptation to a low numerosity (*M* = 229.68 ms, *SD* = 75.50 ms) compared to a high numerosity (*M* = 208.82 ms, *SD* = 57.04 ms) but this difference did not reach statistical significance, $t(11) = 1.71$, $p > 0.05 = 0.11$, Cohen's $d = 0.54$. An estimated Bayes factor suggested that these data were only 0.89 times more likely to occur under a model including an effect of numerosity adaptation with increased adapter size on duration discrimination rather than a model without it. Based on the sequential analysis (Figure 1e), there is no definitive trend found as the data accumulate.

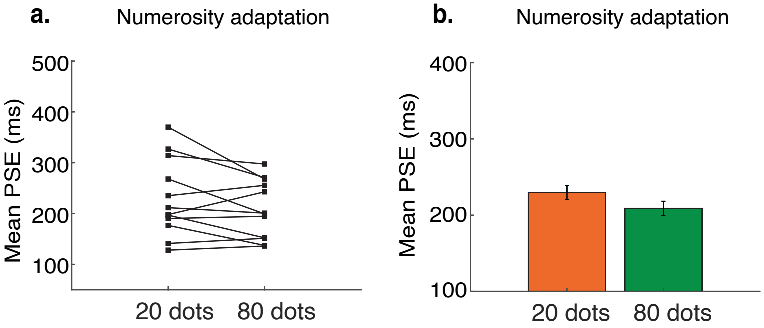
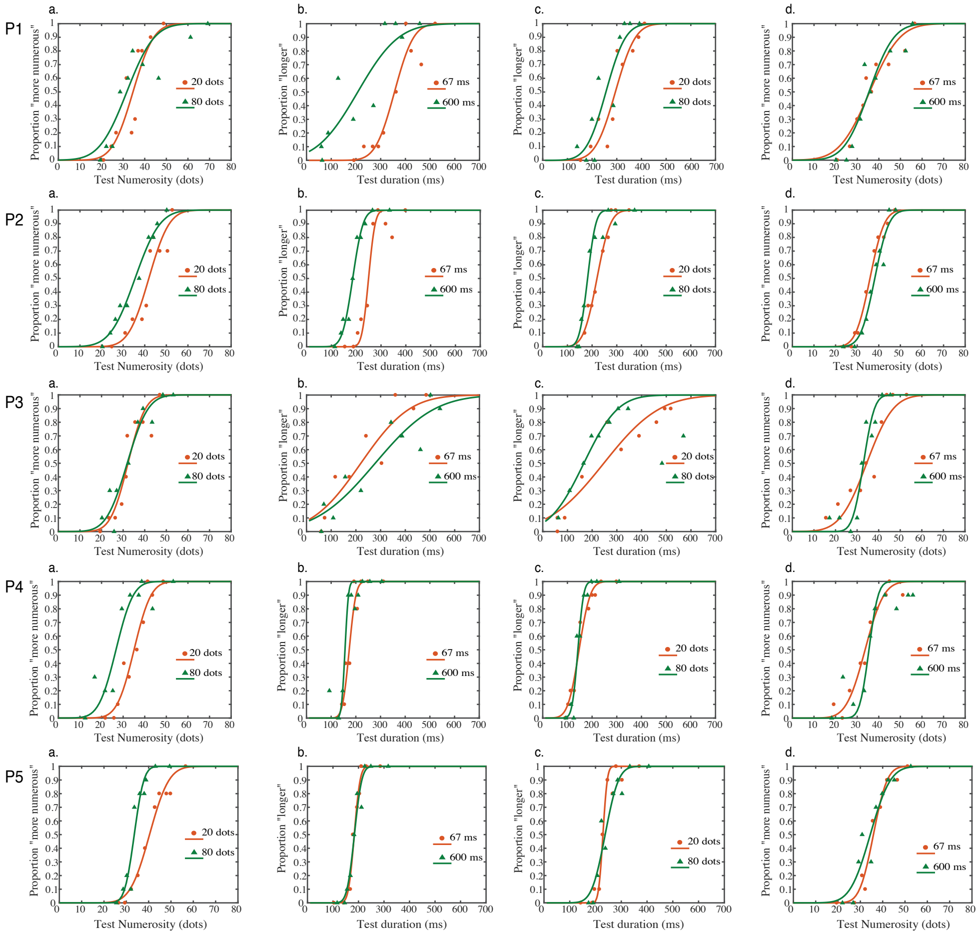
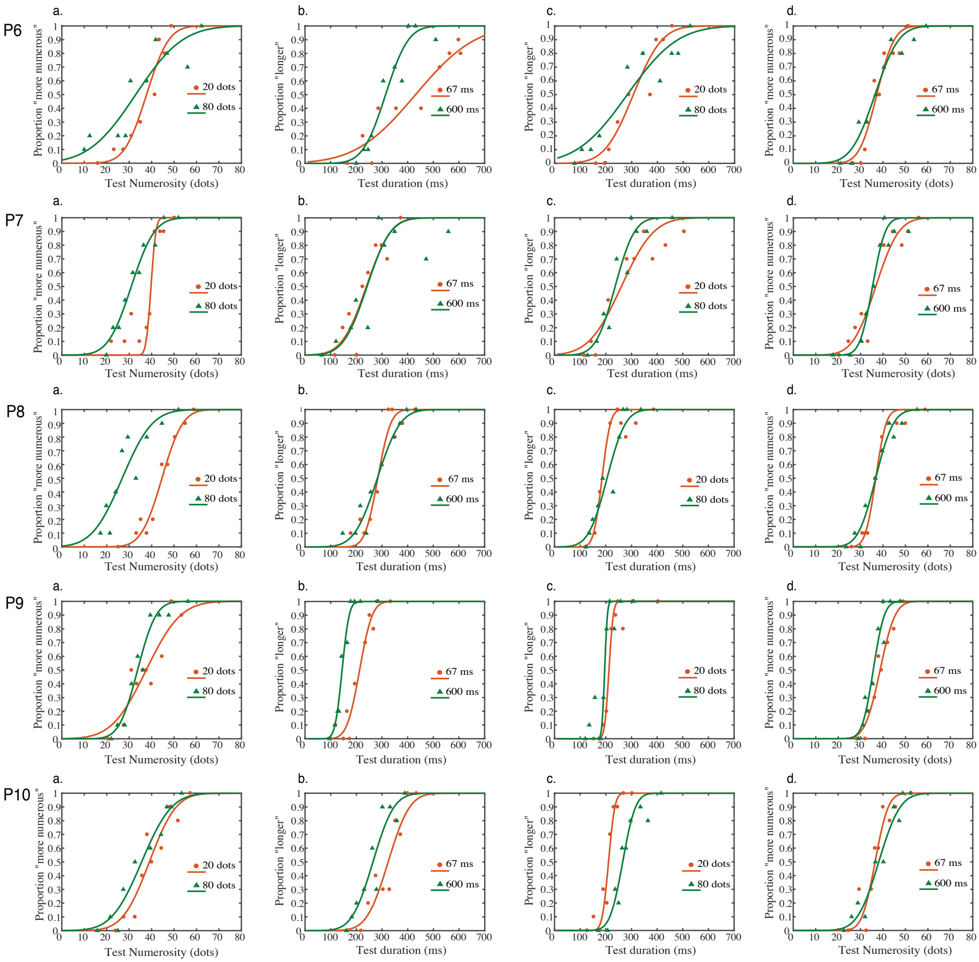


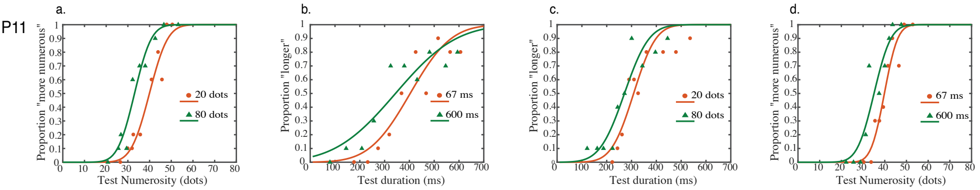
Figure 2. *PSE values for numerosity adaptation-duration discrimination.* (a) PSE values per participant (N = 12) after adapting to numerosity with increased adapter size, and testing on duration discrimination. (b) On a group level, there was no significant effect of numerosity adaptation on duration discrimination.

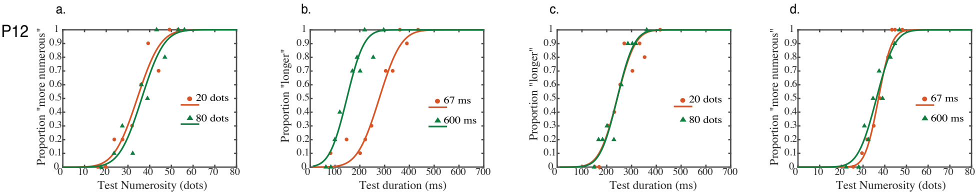
Psychometric curves per participant (columns) and per experiment (rows).

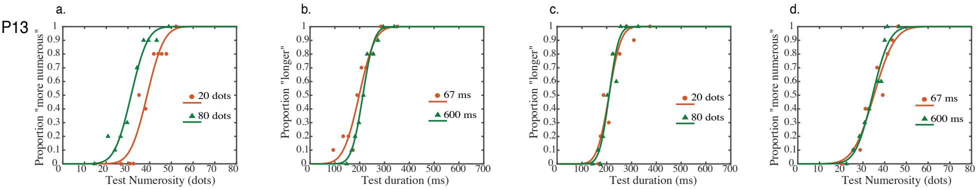
From left to right: (a) numerosity adaptation-numerosity discrimination, (b) duration adaptation-duration discrimination, (c) numerosity adaptation-duration discrimination, (d) duration adaptation-numerosity discrimination.

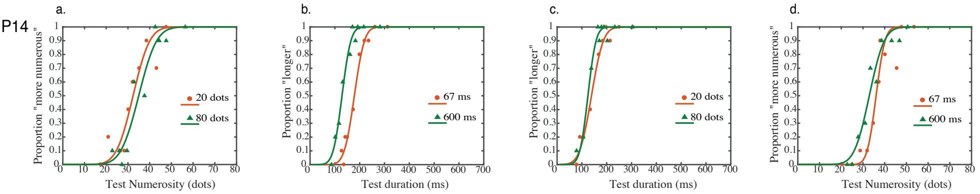


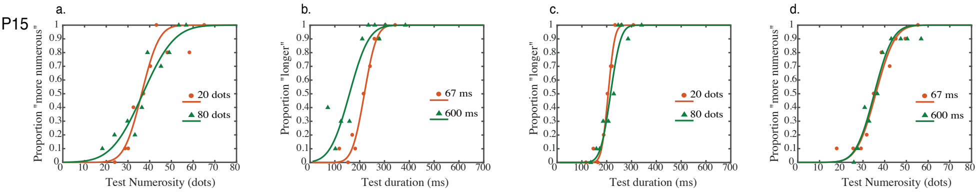

P6
P7
P8
P9
P10
a.
b.
c.
d.
Proportion "more numerous"
Proportion "longer"
Test Numerosity (dots)
Test duration (ms)
20 dots
80 dots
67 ms
600 ms
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
10
20
30
40
50
60
70
80
0
100
200
300
400
500
600
700

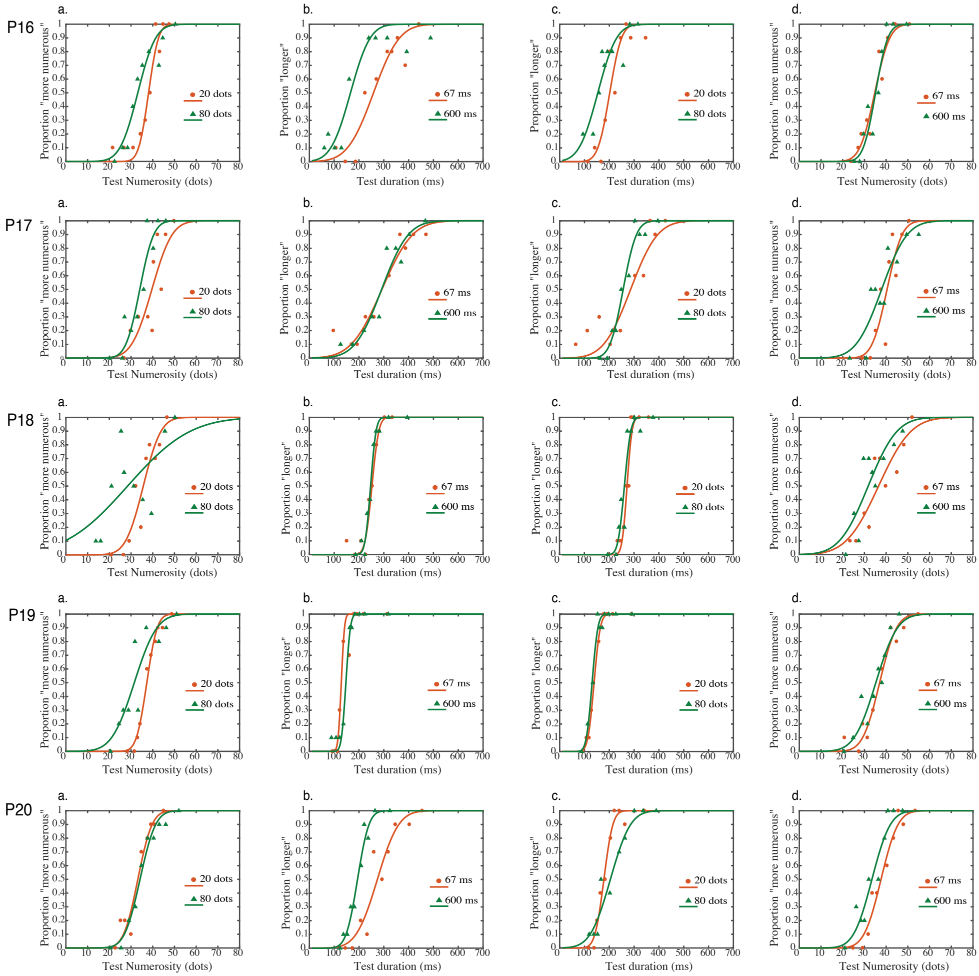

P11
a.
Proportion "more numerous"
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
0 10 20 30 40 50 60 70 80
Test Numerosity (dots)
20 dots
80 dots
b.
Proportion "longer"
0 100 200 300 400 500 600 700
Test duration (ms)
67 ms
600 ms
c.
Proportion "longer"
Test duration (ms)
20 dots
80 dots
d.
Proportion "more numerous"
Test Numerosity (dots)
67 ms
600 ms


P12
a.
Proportion "more numerous"
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
0 10 20 30 40 50 60 70 80
Test Numerosity (dots)
20 dots
80 dots
b.
Proportion "longer"
0 100 200 300 400 500 600 700
Test duration (ms)
67 ms
600 ms
c.
Proportion "longer"
Test duration (ms)
20 dots
80 dots
d.
Proportion "more numerous"
Test Numerosity (dots)
67 ms
600 ms


P13
a.
Proportion "more numerous"
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
0 10 20 30 40 50 60 70 80
Test Numerosity (dots)
20 dots
80 dots
b.
Proportion "longer"
0 100 200 300 400 500 600 700
Test duration (ms)
67 ms
600 ms
c.
Proportion "longer"
Test duration (ms)
20 dots
80 dots
d.
Proportion "more numerous"
Test Numerosity (dots)
67 ms
600 ms


P14
a.
Proportion "more numerous"
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
0 10 20 30 40 50 60 70 80
Test Numerosity (dots)
20 dots
80 dots
b.
Proportion "longer"
0 100 200 300 400 500 600 700
Test duration (ms)
67 ms
600 ms
c.
Proportion "longer"
Test duration (ms)
20 dots
80 dots
d.
Proportion "more numerous"
Test Numerosity (dots)
67 ms
600 ms


P15
a.
Proportion "more numerous"
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
0 10 20 30 40 50 60 70 80
Test Numerosity (dots)
20 dots
80 dots
b.
Proportion "longer"
0 100 200 300 400 500 600 700
Test duration (ms)
67 ms
600 ms
c.
Proportion "longer"
Test duration (ms)
20 dots
80 dots
d.
Proportion "more numerous"
Test Numerosity (dots)
67 ms
600 ms


P16
P17
P18
P19
P20
a.
b.
c.
d.
Proportion "more numerous"
Proportion "longer"
Test Numerosity (dots)
Test duration (ms)
20 dots
80 dots
67 ms
600 ms
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
10
20
30
40
50
60
70
80
100
200
300
400
500
600
700

Chapter 4

Individual participants' data for experiment 1 and 2

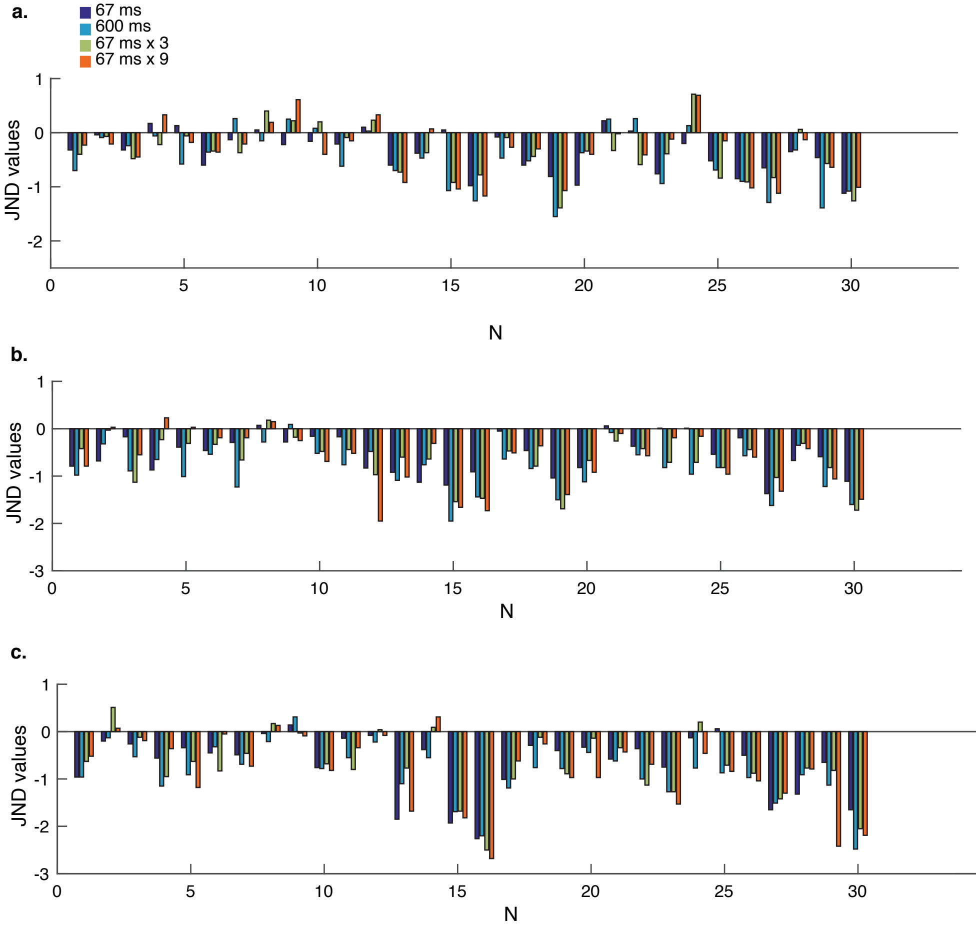


Figure 1. *Individual participants' data for experiment 1 (N = 30).* (a) Adaptation to duration using an adapter and reference stimulus of 20 dots. (b) Adaptation to duration using an adapter and reference stimulus of 40 dots. (c) Adaptation to duration using an adapter and reference stimulus of 80 dots. The colored bars represent the 4 duration conditions. When using 40 dots as a reference and test stimulus (b), the condition with a single long duration (600 ms, blue bars), produced the strongest underestimation effects (compared to the other duration conditions) in most participants, in accordance with the duration/numerosity channels hypothesis.

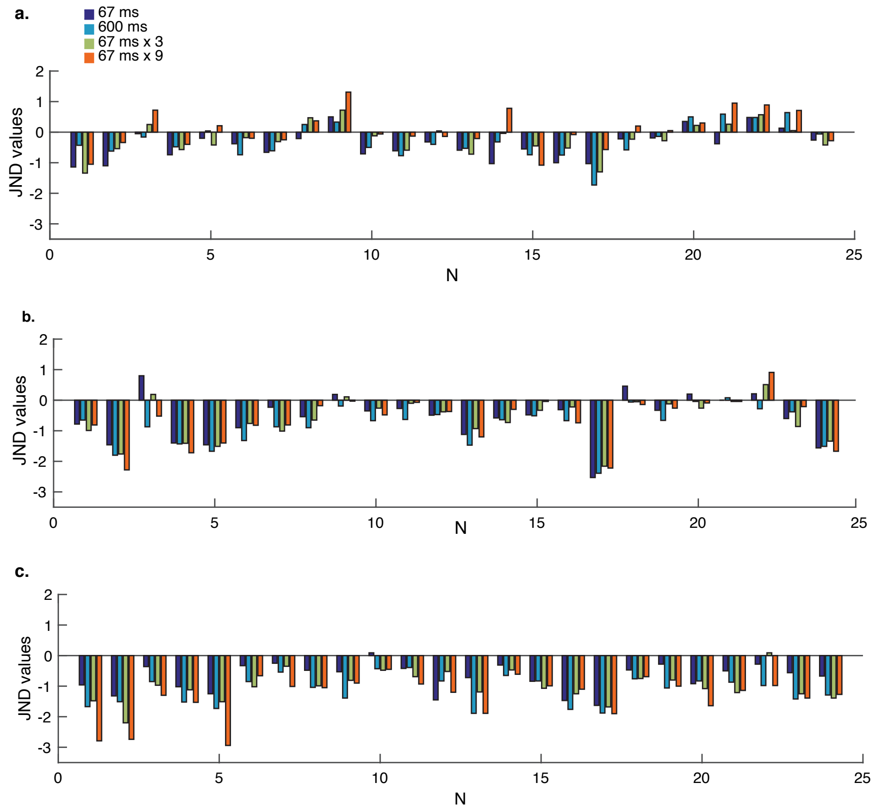
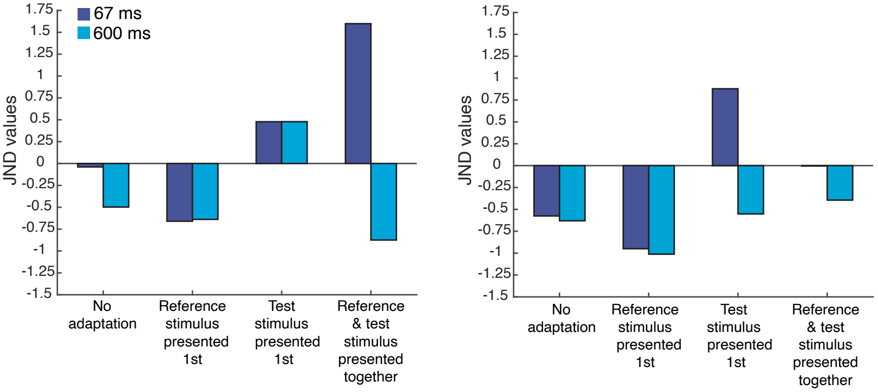
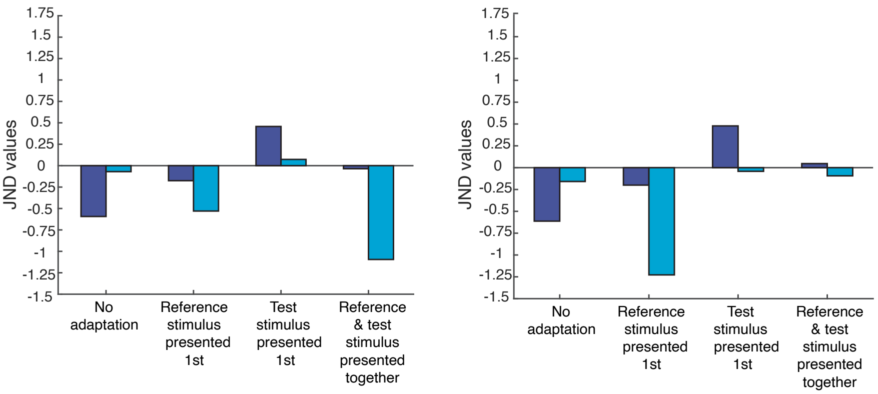


Figure 2. *Individual participants' data for experiment 2* (N = 24). (a) Adaptation to numerosity and duration using an adapter of 20 dots and a reference stimulus of 40 dots. (b) Adaptation to duration using an adapter and reference stimulus of 40 dots. (c) Adaptation to numerosity and duration using an adapter of 80 dots and a reference stimulus of 40 dots. The colored bars represent the 4 duration conditions. When using 20 dots or 80 dots as an adapter stimulus (a, b), the conditions with the longest adapter presentation time (600 ms, blue and orange bars), have produced the strongest adaptation effects in most participants, in accordance with the 'strength'-of-adaptation hypothesis.

Control experiment on the role of a time-order effect (TOE)


a. Participant 1

b. Participant 2


c. Participant 3

d. Participant 4

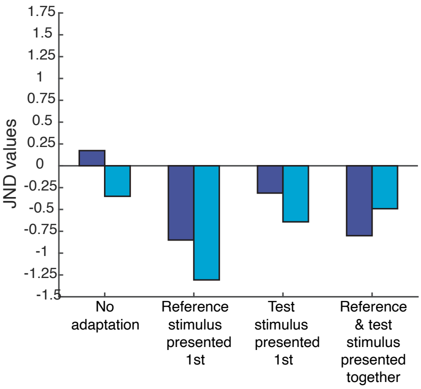

d. Participant 5

Figure 3. *(a-e) Individual participants' data expressed in JND values for the control experiment*. In the majority of participants, and irrespectively of presentation order condition, adapting to a long onset/offset duration (light blue bars) resulted in lower JND values (i.e. underestimation of the reference numerosity), compared to adapting to a short onset/offset duration (dark blue bars).

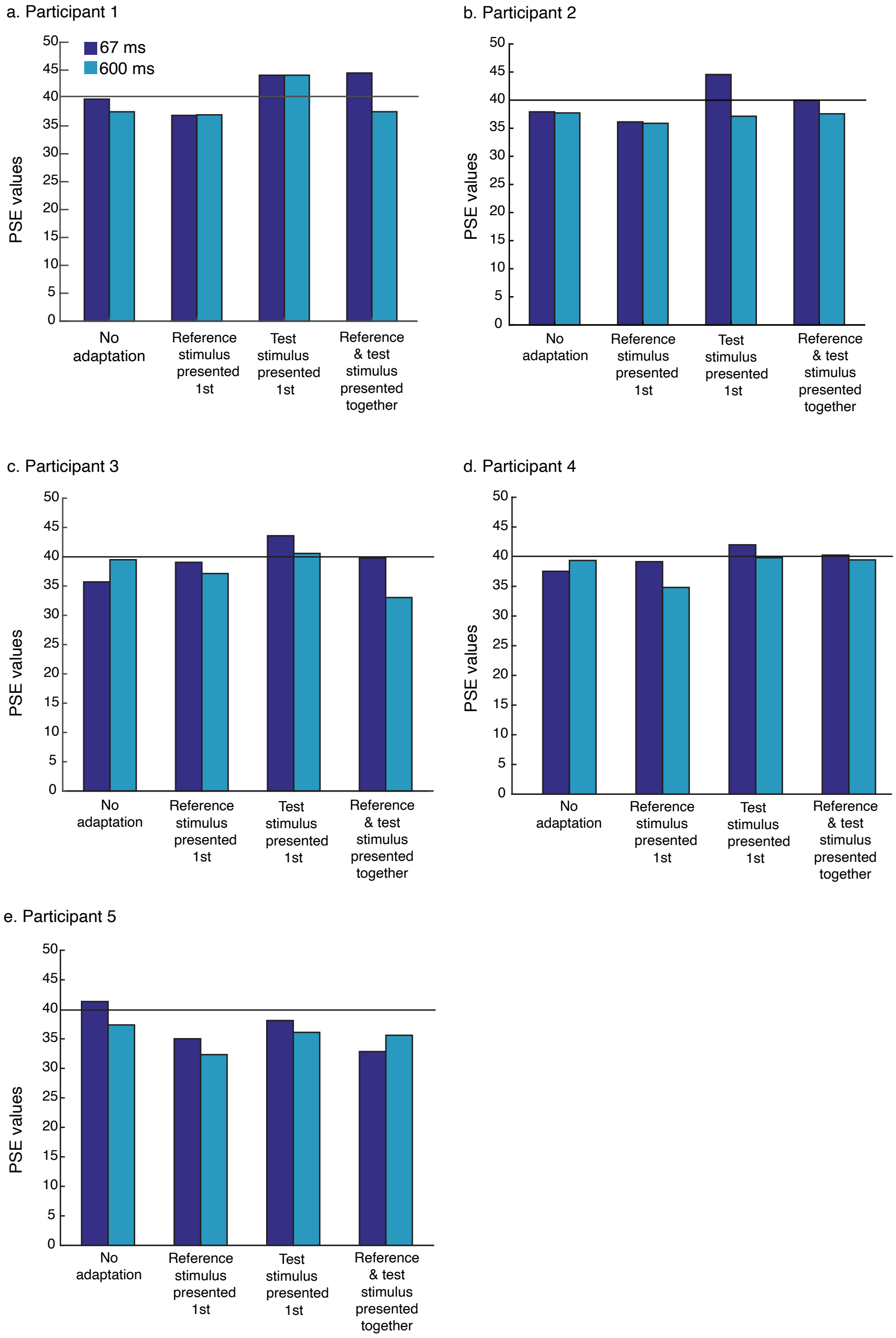


Figure 4. *(a-e) Individual participants' data expressed in PSE values for the control experiment*. In the majority of participants, and irrespectively of presentation order condition, adapting to a long onset/offset duration (light blue bars) resulted in lower PSE values (i.e. underestimation of the reference numerosity), compared to adapting to a short onset/offset duration (dark blue bars).

Appendix

Summary in Dutch

Summary in Dutch

Het menselijk vermogen om hoeveelheden snel en intuïtief in te schatten is evolutionair geconserveerd en ook bij vele niet-menselijke diersoorten (Cantlon & Brannon, 2007; Ditz & Nieder, 2016; Jones et al., 2014; Miletto et al., 2016; Nieder et al., 2002) en bij kleine kinderen aanwezig (Barth et al., 2005; Izard et al., 2009; Schleger et al., 2014; Xu & Spelke, 2000). Dit 'gevoel voor hoeveelheden' (Dantzig, 1930; Dehaene, 2011) is van evolutionair belang om te kunnen navigeren, voedselbronnen te exploiteren en predatie te vermijden (Nieder, 2020b).

De verwerking van aantallen is gebaseerd op de activiteit van neuronen die bij voorkeur reageren op, of 'selectief' zijn voor, een bepaalde hoeveelheid (Burr & Ross, 2008; Nasr et al., 2019; Viswanathan & Nieder, 2013). Deze individuele neuronen zijn experimenteel aangetoond bij mensen (Kutter et al., 2018), apen (Nieder & Miller, 2003, 2004a; Viswanathan & Nieder, 2013) en kraaien (Wagener et al., 2018). De respons van deze neuronen is maximaal wanneer een specifieke hoeveelheid wordt gepresenteerd, d.w.z. de voorkeurshoeveelheid, en neemt af naar mate het verschil tussen de voorkeurshoeveelheid en de aangeboden hoeveelheid groter wordt.

Bij mensen werd deze neurale selectiviteit voor hoeveelheden voor het eerst aangetoond met behulp van functionele magnetische resonantie beeldvorming (fMRI) adaptatie (Piazza et al., 2004). Deze methode maakt gebruik van de verminderde bloed-zuurstof-niveau-afhankelijke (BOLD) respons die gepaard gaan met de herhaalde presentatie van een specifieke stimulus. Wanneer er vervolgens een andere stimulus wordt gepresenteerd herstelt de respons weer (Grill-Spector et al., 2006; Krekelberg et al., 2006; Larsson et al., 2016). Voor hoeveelheden was deze afname van de respons een functie van het verschil in hoeveelheid. Dit komt overeen met een neurale selectiviteit voor hoeveelheden (He et al., 2015; Jacob & Nieder, 2009; Kersey & Cantlon, 2017; Piazza et al., 2004).

Neurale selectiviteit voor hoeveelheden, en de corticale organisatie hiervan, zijn sindsdien directer gemeten door Harvey en collega's (2013) met behulp van ultra-hoog veld (7 Tesla) fMRI en biologisch geïnspireerde modellen (populatie receptief veld [pRF]-modellering; Dumoulin & Wandell, 2008; Wandell & Winawer, 2015). Deze studie toonde neurale populaties aan die selectief zijn voor lage aantallen, in de (rechter) pariëtale hersenschors. Deze neurale populaties bleken op een zeer gestructureerde manier te zijn georganiseerd, door middel van een een topografische hoeveelheidskaart (Harvey et al., 2013), vergelijkbaar met een liniaal. Daaropvolgende studies onthulden het bestaan van zes topografische kaarten van hoeveelheden in de linker- en rechterhersenhelft (Harvey & Dumoulin, 2017a), evenals een continue neurale representatie van lage en hoge hoeveelheden binnen dezelfde kaarten (Cai et al., 2021).

Neurale selectiviteit wordt ook onderzocht met behulp van psychofysica en adaptatie. In de psychofysica wordt adaptatie gebruikt om te onderzoeken hoe de recente zintuiglijke geschiedenis de perceptuele ervaring beïnvloedt door de herhaalde presentatie van een bepaalde stimulus, waardoor vervolgens gepresenteerde stimuli meer van de adapter lijken te verschillen dan het geval is (Frisby, 1979; Kohn, 2007; Mollon, 1974; Thompson & Burr, 2009). Adaptatie berust op het principe dat een bepaalde stimulusparameter wordt gecodeerd door populaties van neuronen of 'kanalen' die zijn afgestemd op verschillende waarden van die parameter en die verschillende maar overlappende selectiviteitscurves hebben. Herhaalde of langdurige blootstelling aan een specifieke stimuluswaarde wordt geacht de respons van voor deze waarde selectieve neuronen te onderdrukken, waarbij de mate van onderdrukking afhankelijk is van hoe sterk de neuronen op die waarde reageren (Clifford et al., 2000; Jin et al., 2005; Thompson & Burr, 2009). Het kenmerk van deze door adaptatie geïnduceerde verandering in neurale respons is dat deze selectief is, aangezien de neurale respons worden onderdrukt voor waarden die vergelijkbaar zijn aan de geadapteerde waarde, maar niet voor waardes die voldoende verschillen (Webster, 2015). Aangenomen wordt dat deze selectieve responsonderdrukking zorgt dat de waarde van een geëncodeerde stimulusparameter verschuift (weg van de geadapteerde waarde), hetgeen vervolgens tegengestelde perceptuele na-effecten voorspelt bij waarden die iets onder of boven de geadapteerde waarde liggen (Webster, 2011). Daarom is adaptatie een waardevolle methode voor het onderzoeken van ervaringsafhankelijke perceptuele plasticiteit die kan worden gekoppeld aan adaptatie-geïnduceerde plasticiteit van neurale selectiviteit voor een bepaalde sensorische eigenschap (Dragoi et al., 2000, 2001; Kohn & Movshon, 2004; Tolias et al. ., 2005). Hoeveelheid is, net als andere visuele eigenschappen zoals kleur of contrast, vatbaar voor adaptatie, wat tegengestelde na-effecten oplevert (zie Anobile et al., 2016 voor een overzicht). Concreet leidt adaptatie aan een kleine hoeveelheid tot een overschatting van de hoeveelheid die vervolgens op de geadapteerde locatie (in het visuele veld) wordt gepresenteerd, terwijl adaptatie aan een groete hoeveelheid juist tot een onderschatting leidt (Burr et al., 2017; Burr & Ross, 2008). Deze perceptuele afstoting van de adapter wordt vaak gebruikt om selectiviteit van neurale reacties op een geadapteerde stimuluseigenschap te demonstreren, omdat wordt verondersteld dat het de responsamplitude van een deel van de neurale selectiviteitsfunctie vermindert, waardoor de optimale stimulus (ofwel selectiviteit) als het ware wordt weggeduwd van de adapter. Ondanks de grote hoeveelheid onderzoeken naar selectiviteit voor hoeveelheden met behulp van psychofysica en adaptatie (zie Anobile et al., 2016 voor een overzicht), begrijpen we nog maar weinig van hoe het hoeveelheidsna-effect neuronaal tot stand komt. Het is bijvoorbeeld momenteel nog onduidelijk of de perceptuele effecten van hoeveelheidsadaptatie verband houden met veranderingen in het selectiviteitssprofiel van de hoeveelheids-selectieve neuronen.

Om optimaal te kunnen functioneren in onze omgeving, moeten we informatie verwerken over hoeveelheid maar ook andere grootheden, zoals tijd en ruimtelijke maten (bijvoorbeeld fysieke grootte, lengte en afstand). Tijd blijft een van de meest ongrijpbare en veelzijdige grootheden, en het blootleggen van de neurale en computationele basis hiervan wordt gekarakteriseerd als de "heilige graal" van onderzoek naar tijdswaarneming (Matell, 2014). Er zijn verschillende schalen van tijdswaarneming, variërend van microseconden tot circadiaanse ritmes (Mauk & Buonomano, 2004). In dit proefschrift concentreer ik me op tijdsintervallen in het sub-seconde bereik, ook wel 'perceptual timing' genoemd (Buonomano & Karmarkar, 2002).

Uit elektrofysiologische, psychofysische en fMRI-onderzoeken komen aanwijzingen voor het bestaan van tijdsselectieve neurale substraten, waarbij temporele informatie wordt gecodeerd door afzonderlijke kanalen of neurale populaties die zijn afgestemd op specifieke, voorkeursduren. Elektrofysiologische studies bij dieren hebben neuronen aangetoond die zijn afgestemd op bepaalde tijdsintervallen van enkele honderden milliseconden (Duysens et al., 1996; Jin et al., 2009; Merchant et al., 2013). Bij mensen werd 'duurselectiviteit' voor het eerst gedemonstreerd met behulp van psychofysica en adaptatie (Heron, Aaen-Stockdale, et al., 2012). Heron en collega's (2012) toonden het bestaan van het na-effect van duur aan, waarbij de herhaalde presentatie van een korte (160 ms) versus lange (640 ms) duur leidt tot respectievelijk over- versus onderschatting van een latere, in dezelfde modaliteit gepresenteerde, duur (Heron, Aaen-Stockdale, et al., 2012). Ultra-high field (7 Tesla) fMRI-onderzoek bij mensen heeft het bestaan aangetoond van op duur afgestemde neurale populaties die topografisch zijn georganiseerd (Harvey et al., 2020; Protopapa et al., 2019).

Een aantal theorieën (Bonn & Cantlon, 2012; Church & Broadbent, 1990; Gallistel & Gelman, 2000; Walsh, 2003) stellen dat verschillende grootheden zoals hoeveelheid en duur van dezelfde computationele en/of neurale mechanismen gebruikmaken. Deze theorieën worden ondersteund door neuroimaging-bevindingen die overlappende hersenactiviteit laten zien tijdens taken met verschillende grootheden (Cantlon et al., 2009; Cohen Kadosh et al., 2008; Sokolowski et al., 2017) en perceptuele interacties tussen grootheden. Maar overlappende hersenactiviteit impliceert nog niet dat één gemeenschappelijke neurale code voor verschillende grootheden hieraan ten grondslag ligt, en recente gedragsstudies die de interactie van hoeveelheid en tijd onderzoeken als onderdeel van één gemeenschappelijk 'magnitude-systeem' suggereren een complexe relatie tussen deze grootheden, als deze al aanwezig is (zie Hamamouche & Cordes, 2019 voor een overzicht).

Uit het bovenstaande volgt het algemene doel van het onderzoek in dit proefschrift. Wat zijn de eigenschappen van neurale populaties die selectief zijn voor hoeveelheden

(**Hoofdstuk 2**), en is waarneming van hoeveelheden een onderdeel van een gegeneraliseerd 'magnitude-systeem'? Worden de selectieve mechanismen voor hoeveelheden en tijd echt 'gedeeld' (**Hoofdstukken 3** en **4**), en is dit het geval voor andere grootheden en zintuiglijke modaliteiten (**Hoofdstuk 5**)?

In **Hoofdstuk 2** bouwen we voort op eerdere onderzoeksresultaten (Harvey et al., 2013; Harvey & Dumoulin, 2017a) die het bestaan aantonen van topografisch georganiseerde neurale populaties die zijn afgestemd op visuele hoeveelheden in het menselijk brein. We onderzoeken of neurale selectiviteit voor visuele hoeveelheden binnen het netwerk van kaarten van hoeveelheden kan worden veranderd door te adapteren aan specifieke aantallen. We veronderstelden dat als de selectiviteit van de neurale populaties wordt beïnvloed door adaptatie, hun voorkeurshoeveelheid zou veranderen, afhankelijk van of er is geadapteerd en het specifieke aantal waarmee is geadapteerd. We scanden deelnemers met behulp van ultra-hoog field (7 Tesla) fMRI en analyseerden de hersenactiviteit met behulp van zelf-ontwikkelde neurale pRF modellen. We repliceerden de eerdere studies door het bestaan van verschillende topografische hoeveelheidskaarten aan te tonen en lieten verder zien dat de neurale selectiviteit voor hoeveelheid systematisch wordt veranderd in alle hoeveelheidskaarten tijdens adaptatie. We suggereren dat deze veranderingen in neurale selectiviteit mogelijk ten grondslag liggen aan de perceptuele effecten van adaptatie.

In **Hoofdstuk 3** onderzoeken we met behulp van psychofysica en een paradigma van cross-adaptatie of de verwerking van hoeveelheden en tijd afhankelijk zijn van gemeenschappelijke neurale mechanismen. We redeneerden dat als waarneming van hoeveelheden en tijdsduur afhankelijk zijn van dezelfde neurale substraten, adaptatie aan visuele hoeveelheden de visuele tijdsduurwaarneming zou moeten beïnvloeden, en adaptatie aan visuele tijdsduur de visuele hoeveelheidswaarneming zou moeten beïnvloeden. We repliceerden eerdere bevindingen door aan te tonen dat zowel waarneming van hoeveelheden als van tijdsduur vatbaar zijn voor adaptatie. We laten verder zien dat tijdsduuradaptatie een tegengesteld perceptueel na-effect produceert bij hoeveelheidswaarneming, terwijl adaptatie aan hoeveelheden geen significante invloed heeft op tijdsduurwaarneming. We suggereren dat de verwerking van hoeveelheden en tijdsduur afhankelijk zijn van gedeeltelijk overlappende neurale netwerken.

In **Hoofdstuk 4** gaan we dieper in op het effect van tijdsduuradaptatie op de hoeveelheidswaarneming, door twee vervolgexperimenten uit te voeren, weer met behulp van psychofysica en adaptatie. In het eerste experiment testten we het effect van tijdsduuradaptatie op visuele hoeveelheidswaarneming, en in het tweede experiment testten we het gecombineerde effect van adaptatie aan zowel visuele tijdsduur als hoeveelheid op visuele hoeveelheidswaarneming. We manipuleerden de tijdsduur van de adapter, de totale presentatietijd van de adapter en de totale tijdsduur van de adaptatieconditie. We veronderstelden dat als het effect van tijdsduur op hoeveelheden de adaptatie van tijdsduurkanalen weerspiegelt die zijn afgestemd op specifieke tijdsduur, het effect van adaptatie zal worden bepaald door de tijdsduur van de adapter. Als daarentegen het effect van de tijdsduur slechts de adaptatiesterkte van alleen hoeveelheidskanalen weerspiegelt, dan zal het adaptatie-effect worden bepaald door de totale duur van de adaptatieconditie, ongeacht van de tijdsduur van de adapter. We laten zien dat het effect van tijdsduuradaptatie op hoeveelheidswaarneming wordt bepaald door het adapteren van specifieke tijdsduurkanalen, terwijl het effect van hoeveelheidsadaptatie op hoeveelheidswaarneming wordt bepaald door de totale duur van de adaptatieconditie. We suggereren dat bij tijdsduuradaptatie en hoeveelheidsadaptatie verschillende 'temporele mechanismen' betrokken zijn.

In **Hoofdstuk 5** verbreden we de discussie van de neurale selectiviteit bij hoeveelheidswaarneming naar andere grootheden en zintuiglijke modaliteiten. We stellen dat neurale selectiviteit de (neurale) basis is van de verwerking van grootheden in het algemeen, en van cruciaal belang is voor het begrijpen hiervan. Onze hypothese is gebaseerd op gevestigde theorieën uit de visuele waarnemingswetenschap en verbindt recente resultaten van elektrofysiologie bij dieren, neuro-imaging bij mensen en psychofysica met waarneming van hoeveelheden. We stellen dat de neurale selectiviteit nauw verbonden is met waarneming en onderliggende psychofysische wetten en gedragseffecten bij waarneming van hoeveelheden. We stellen verder dat neurale selectiviteit de basis is voor perceptuele interacties tussen verschillende hoeveelheden en modaliteiten. Op basis hiervan suggereren we dat waargenomen overeenkomsten in neurale en gedragsrepresentaties tussen verschillende grootheden niet worden verklaard door het bestaan van neurale populaties die selectief zijn voor meerdere grootheden, maar door de interactie van neurale populaties op nabijgelegen locaties in het brein die onafhankelijk selectiviteit vertonen voor verschillende grootheden.

Conclusie

De bevindingen van dit proefschrift dragen bij aan ons begrip van de eigenschappen van neurale selectiviteit voor hoeveelheden en laten verder zien hoe mechanismen voor hoeveelheden interacteren met mechanismen voor tijdsduur. Bovendien, en op basis van bewijs dat het bestaan aantoont van neurale populaties die selectief reageren op verschillende grootheden en in verschillende sensorische modaliteiten, stellen we voor dat neurale selectiviteit voor kwantiteit fundamenteel is voor kwantiteitswaarneming. We suggereren verder dat neurale selectiviteit een cruciaal mechanisme is voor het begrijpen van de neurale basis van perceptuele interacties tussen verschillende soorten grootheden.

Uiteindelijk bieden de implicaties van wat in dit proefschrift wordt behandeld een antwoord op de vraag waarom cognitieve wetenschappers zich zorgen moeten maken over neuronen, en bieden ze het raamwerk voor nieuwe onderzoeksrichtingen. Dus: Blijf kijken voor meer (of minder).

Appendix

Acknowledgments

Acknowledgments

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Appendix

List of publications

List of publications

Published peer-reviewed articles:

Tsouli, A., Harvey, B. M., Hofstetter, S., Cai, Y., van der Smagt, M. J., te Pas, S. F., & Dumoulin, S. O. (2022). The role of neural tuning in quantity perception. *Trends in Cognitive Sciences, 26*(1), 11–24. https://doi.org/10.1016/j.tics.2021.10.004

Tsouli, A., Cai, Y., van Ackooij, M., Hofstetter, S., Harvey, B. M., te Pas, S. F., van der Smagt, M. J., & Dumoulin, S. O. (2021). Adaptation to visual numerosity changes neural numerosity selectivity. *NeuroImage*, *229*, 117794. https://doi.org/10.1016/j.neuroimage.2021.117794

Tsouli, A., Dumoulin, S. O., te Pas, S. F., & van der Smagt, M. J. (2019). Adaptation reveals unbalanced interaction between numerosity and time. *Cortex*, *114*, 5–16. https://doi.org/10.1016/j.cortex.2018.02.013

Tsouli, A., van der Smagt, M. J., Dumoulin, S. O., & Te Pas, S. F. (2019). Distinct temporal mechanisms modulate numerosity perception. *Journal of Vision*, *19*(6), 19. https://doi.org/10.1167/19.6.19

de Zwarte, S. M. C., Brouwer, R. M., **Tsouli, A.**, Cahn, W., Hillegers, M. H. J., Hulshoff Pol, H. E., Kahn, R. S., & van Haren, N. E. M. (2019). Running in the Family? Structural Brain Abnormalities and IQ in Offspring, Siblings, Parents, and Co-twins of Patients with Schizophrenia. *Schizophrenia Bulletin*, *45*(6), 1209–1217. https://doi.org/10.1093/schbul/sby182

Loi, M., Sarabdjitsingh, R. A., **Tsouli, A.**, Trinh, S., Arp, M., Krugers, H. J., Karst, H., van den Bos, R., & Joëls, M. (2017). Transient Prepubertal Mifepristone Treatment Normalizes Deficits in Contextual Memory and Neuronal Activity of Adult Male Rats Exposed to Maternal Deprivation. *ENeuro*, *4*(5), ENEURO.0253-17.2017. PubMed. https://doi.org/10.1523/ENEURO.0253-17.2017

Tsouli, A., Pateraki, L., Spentza, I., & Nega, C. (2017). The effect of presentation time and working memory load on emotion recognition. *Journal of Psychology and Cognition*, *2*(1), 61-66. https://doi.org/10.35841/psychology-cognition.2.1.61-66

Appendix

Curriculum Vitae

Curriculum Vitae

Andromachi (Ada) Tsouli was born on the 9th of November 1989 in Athens, Greece. After graduating from secondary school in 2008, she completed a Bachelor of Arts (Hons) at DEREE – The American College of Greece, where she majored in psychology and minored in biology (summa cum laude, class valedictorian). Following this, she moved to Utrecht where she completed a Master of Science in neuroscience and cognition (cum laude) at Utrecht University. In 2016, she started her PhD project at the department of Experimental Psychology of Utrecht University and the Spinoza Centre for Neuroimaging in Amsterdam, under the supervision of Prof. dr. Maarten J. van der Smagt (promotor), Prof. dr. Susan F. te Pas (co-promotor), and Prof. dr. Serge O. Dumoulin (co-promotor). Currently, Ada is looking for her next step in her career outside academia.