Number adaptation: reply

David Burr, Giovanni Anobile & Roberto Arrighi

Department of Neuroscience, University of Florence, Italy

Abstract

Adaptation is a ubiquitous property of perceptual systems, allowing them to operate over a large dynamic range, and increasing sensitivity to change. The *number sense*, like most other perceptual systems, shows strong adaptation. In this issue, Yousef et al challenge the existence of number adaptation, offering an alternate explanation that they term the "old news hypothesis". Here we consider the major evidence for their claims and show that, while their predicted effects may reach statistical significance, they are far too small to begin to explain the robust phenomenon of adaptation. We also highlight a series of studies using fMRI, EEG, pupillometry and psychophysical techniques that support the existence of adaption, and are inconsistent with "old news". We conclude that number adaptation, while not entirely understood, remains an invaluable concept for understanding the *number sense*.

Number adaptation: reply

Abstract

Adaptation is a ubiquitous property of perceptual systems, increasing sensitivity to change and allowing them to operate over a large dynamic range. The *number sense*, like most other perceptual systems, is adaptable. In this issue, Yousef et al challenge the existence of number adaptation, offering an alternate explanation that they term the "old news hypothesis". Here we consider the major evidence advanced for their theory and show that, while their predicted effects may reach statistical significance, they are far too small to begin to explain the robust phenomenon of adaptation. We also highlight a series of studies using fMRI, EEG, pupillometry and psychophysical techniques that support the existence of adaption, and are inconsistent with "old news". We conclude that number adaptation, while not fully understood, does indeed exist, and remains an invaluable concept for understanding the *number sense*. It is flattering that sixteen years after our initial demonstration of adaptation to number (Burr & Ross, 2008), enterprising researchers find the theme of sufficient interest to forward a novel interpretation. While we do not agree with their conclusions, we accept that fresh approaches may lead to new research, and possibly new insights. However, as this reply makes clear, the notion of adaptation of numerosity, clearly a primary perceptual attribute, has been far from refuted. We highlight critical physiological and psychophysical data collected from several laboratories over the past years, and report a couple of experiments designed specifically to examine Yousif et al.'s ideas. The reply is not intended to treat all their arguments exhaustively, but to provide a quantitative analysis of the more critical issues.

Physiological Evidence

While Yousif et al's (2024) review of the literature was extensive, they omitted several important relevant studies that are difficult to explain without the concept of adaptation. An obvious example is the use of adaptation to study the neural underpinnings of numerosity representation in humans (Piazza et al., 2004). Adapting to a specific number of dots (say 16) reduces the fMRI BOLD response to subsequent presentations of 16 stimuli, but less to stimuli containing more or fewer dots, revealing tuning to number in human interparietal sulcus (hIPS). Later studies demonstrated cross-modal neural adaptation, adapting to dot-patterns and testing with Arab digits, and *vice versa* (Piazza et al., 2007).

Piazza's studies relied on *neural* adaptation as the technique to demonstrate number tuning in humans. Castaldi et al (2016) used classification techniques to decode numerosity from BOLD signals in area hIPS. They successfully decoded numerosity both before and after adaptation, provided that both training and testing of the algorithm used signals from the same condition (before or after adaptation): classifiers trained on non-adapted stimuli could not decode signals after adaptation, and vice versa. This clearly shows that the neural representation of number was altered by adaptation, to the point where otherwise successful classifiers fail. It is not clear exactly how "old news" or "item adaptation" may explain the change in neural representation revealed by these and other fMRI studies. The P2p ERP potential (latency around 200 ms), known to be modulated by numerosity (Fornaciai & Park, 2017; Hyde & Spelke, 2012), is strongly modulated by adaptation to numerosity (Grasso, Petrizzo, et al., 2022). Furthermore, the effects of number adaptation on EEG can be decoded by classification techniques, and participants with strongest adaptation to number show best decoding accuracy of adaptation signals (Ranieri et al., 2023). Again, the results show that adaptation changes the neural representation to numerosity of spatial arrays, not only perception (or response bias).

And there is pupillometric evidence. The gain of the pupillary response to light and dark stimulation (a very basic reflex) is modulated by the apparent numerosity of the stimuli, consistent with numerosity being a very basic attribute to which the brain responds spontaneously (Castaldi et al., 2021). After adaptation to low or high numerosities, the gain modulation changes appropriately, consistent with a change in the neural representation (Caponi, Castaldi, Burr, et al., 2024).

These studies, using magnetic resonance, EEG and pupillometry, all point to adaptationinduced changes in neural representations, accompanying the strong perceptual changes revealed by robust behavioural means.

Cross-modal adaptation

Yousif et al's (2024) review correctly observes that the cross-modal adaptation studies provide the clearest evidence for direct adaptation of number, as well as showing that the *number sense* generalizes over space and time, and sensory modality. Arrighi et al (2014) reported bidirectional adaptation to temporal sequences of visual stimuli, as well as cross modal adaptation: auditory to visual and vice versa. Grasso et al (2024) replicated the auditory results, and Togoli and Arrighi (2021) have extended the finding to include tactile stimuli. Arrighi et al (2014) also described *cross-format* adaptation, where adapting to temporal sequences changes the apparent numerosity of spatial arrays. Later, Anobile et al (2016) extended this concept further to include action, showing that adaptation to slow and fast tapping robustly and bidirectionally changed the apparent numerosity of both temporal sequences and spatial arrays (later confirmed under different conditions: Anobile et al., 2020; Maldonado Moscoso et al., 2020; Yang et al., 2024). That *eight* independent studies, with different adaptation conditions, different laboratories, different participants, and different lead authors, all reported that temporal adaptation (by sensory stimulation or action) strongly affects apparent numerosity of both temporal sequences and of spatial arrays, gives us a certain level of confidence in the phenomenon. It is difficult to understand why Yousif et al are unable to replicate one specific condition (audio-visual adaptation), but we have repeatedly offered to provide full details of our experimental procedures, and any other useful help. We have never had a case of non-replication, even in the hands of undergraduates doing a student project.

Is adaptation perceptual or a response bias?

Yousif et al (2024) reasonably ask whether the effects we term adaptation reflect perceptual processes, or are merely response biases. That they are spatially specific strongly implicates perceptual processes, as a generalized response bias should extend to all stimuli in all positions. In the publications cited above, spatial specificity was examined by measuring adaptation on stimuli presented either in the same or contralateral position as the adapting stimuli or tapping hand, interleaved within the same experiment. In all cases the adaptation occurred only when the positions coincided, not when contralateral. Spatial specificity points to a perceptual, rather than decisional effect. In addition, the intermingled non-congruent condition acts as an internal check, showing that participants selectively reported effects only when they occurred, which is reassuring with untrained, naïve observers.

Zimmermann (2018) went further and measured the spatial tuning for adaptation to both high and low numbers to map out the "perceptive field" for numerosity (Figs 1a): moderately large compared with receptive fields of early visual cortex (about 15° full width half height), but nevertheless clearly circumscribed and orderly. Large perceptive fields are consistent with processing of number occurs in parietal cortex. Interestingly, when he repeated the study with a dense field (100 dots), thought to be encoded by separate, density-based mechanisms of early vision (Burr et al., 2017), the perceptive fields were much smaller, consistent with processing at earlier cortical levels. Figure 1bc show similar characterizations of perceptive fields after adaptation by spatial arrays, visual sequences and hand-tapping, to both spatial arrays and temporal sequences (Anobile et al., 2020). Again, the perceptive fields are well-defined, and quite large (10-30° full-width half-height), consistent with parietal cortex processing.





Spatial tuning of number adaptation. **A.** Spatial tuning of adaptation to spatial arrays of 12 dots, after adaptation to 6 dots (yellow symbols and curves) or to 24 dots (black symbols and curves). Error bars ±1 s.e.m. **B.** Spatial tuning of numerosity changes to dot-arrays after adaptation by dot-arrays (light grey symbols) or hand-tapping (black symbols). Average data were fitted with Gaussian functions (grey and black curves), with the arrows on the abscissa indicating the width of the Gaussian. **C.** Same as B but adapting and testing with sequential stimuli rather than dot arrays. Reproduced with permission from (Anobile et al., 2020) and (Zimmermann, 2018).

Yousif et al (2024) correctly point out that the spatial selectivity is spatiotopic (world- or object-centred), rather than eye- or body-centred. When a saccadic eye movement is interspersed between adaptation and test, the adaptation occurred only when the adaptor and test stimuli were in the same spatial position, irrespective of the retinal position (Arrighi et al., 2014); and if the left hand tapped in the right visual field, the right (not the left) field was adapted (Anobile, Arrighi, et al., 2016). Yousif et al. argue that the spatiotopic nature of the selectivity somehow weakens the case for perceptual adaption: but this reasoning escapes us. There is increasing evidence that many areas in the parietal cortex have spatiotopic rather than retinotopic selectivity (Burr & Morrone, 2012; Crespi et al., 2011; d'Avossa et al., 2007;

Duhamel et al., 1997; Galletti et al., 1993). Many important forms of adaptation have been shown to be spatiotopic, including adaptation of temporal duration (Burr et al., 2007, 2011), the motion-position aftereffect (Mikellidou et al., 2017; Turi & Burr, 2012) and trans-saccadic integration (Drissi-Daoudi et al., 2020). That the selectivity is spatiotopic implicates mid- to high-level analysis, consistent with the number-specific areas such as hIPS, shown to be heavily involved in numerosity perception (Castaldi et al., 2016; Piazza et al., 2004, 2007; Piazza & Eger, 2016). Retinotopy is not a hallmark of adaptation: adaptation to faces or even body size is also strong and robust, but does not require that the adaptor and test overlap physically: they can be of very different sizes or orientations and the effects still hold (somewhat reduced), demonstrating that they do not rely on adaptation to local features at early levels of analysis (Brooks et al., 2018; Rhodes et al., 2009).

Yousif et al. (p28¹) conclude that "It would not be enough to simply show that there are crossmodal effects. One would also have to show that these cross-modal effects are genuinely perceptual (rather than a consequence of some higher-level response bias)". We fully agree! *– extraordinary claims require extraordinary evidence* (LaPlace, 1812). Maldonado Moscoso et al. (2020) adapted a technique devised by Gallagher et al (2019), based on the concept that confidence in a forced-choice judgement should be minimal when psychophysical discriminations are most difficult: by definition, at the point of subjective equality (PSE). If adaptation affects sensory mechanisms, then participants should have least confidence (and longest reaction times) when the test and standard are *perceptually* rather than physically similar. If, on the other hand, adaptation affects only decision criteria, confidence should be minimal at physical similarity (see Fig. 1 of Maldonado Moscoso et al., 2020).

¹ Page numbers refer to the accepted manuscript: they will need updating after pagination of target article.





Evidence that adaptation is perceptual rather than decisional. **A-B**: Psychophysical functions showing proportion of trials in which the test was perceived more numerous than the reference, as a function of test numerosity. The dotted vertical lines pass through the point of subjective equality (PSE), which is displaced by adaptation. **C**-**D**: Confidence levels as a function of test numerosity, for visual and motor adaptation (left and right panels respectively). The minima in these curves shift with adaptation to align to the PSEs. **E-F**: Mean reaction times as a function of test numerosity: The maxima in these curves shift with adaptation to align to the PSEs. **E-F**: Mean reaction times as a function of test numerosity: The maxima in these curves shift with adaptation to align to the PSEs, suggesting that participants have less confidence, and take more time at the adapted PSEs. Arrows show the peaks of the best-fit gaussians to the confidence or reaction time distributions. In all graphs, blue and red curves indicate baseline and high adaptation for visual adaptation (left hand panels) and slow or fast tapping in the motor experiment (right hand panels). Reproduced with permission from (Maldonado Moscoso et al., 2020).

Figure 2 shows the results for adaptation with visual stimuli (a), and to fast and slow tapping (b). Adaptation robustly shifted the psychometric functions, both for visual adaptation and hand-tapping: but crucially, the points of minimum confidence in the judgment (Fig 2c,d), and maximum reaction times (Fig 2e,f) also shifted to align with the points of subjective equality, reinforcing the claim that adaptation had a genuine effect on perception. In a control experiment, when the psychometric functions and PSEs were caused to shift by varying the reward regime (discouraging either "greater than" or "less than" responses), the shift in PSE was not accompanied by a corresponding shift in confidence or reaction time functions. This experiment not only furnishes unequivocal evidence for cross-modal adaptation of

numerosity (the orderly reaction time functions could not be "faked"), but shows that adaptation acts on sensory mechanisms, rather than perceptual decisions or responses.

Dot overlap and reverse adaptation

Yousif et al.'s first major experiment, serving as "proof of principle", was designed to demonstrate "item" rather than "number" adaptation by showing that adaptation occurs principally when adaptation and test dots overlap physically. However, their reported effects were not huge by usual standards in vision research: comparing directly overlapping with non-overlapping adaptation, they found that with overlapping stimuli dots appeared less numerous (more adapted) 59% of the time. Psychophysically, the *just-noticeable-difference* (*JND*, the typical estimate of the perceptual threshold), is defined as the difference in numerosity that supports 75% preference (in two-alternative forced choice). Assuming a cumulative gaussian psychometric function), 59% preference corresponds to $1/3^{rd}$ of a JND. That is to say, *if their effect were three times larger than actually measured, it would become just-noticeable*. Following a referee's objection, they repeated the experiment under more standard conditions for adaptation, with a 400 ms pause between adaptor and test, presumably to minimise forward masking. This further halved the effect to $1/5^{th}$ of a JND – not the most compelling evidence for rejecting decades of adaptation research.





Item adaptation and reverse adaptation. A. Aggregate psychometric functions comparing adaptation effects when the dots in the reference stimulus were constrained to the same positions as the adaptor ("full overlap", yellow curves), or to the gaps in between ("no overlap", red curves), or allowed to fall anywhere by chance ("incidental", blue curves). Black curves show the baseline, with no adaptation. The adapters comprised 100 dots (half white half black), presented to the right of a central fixation point, for 5 s in each trial. After a 500 ms pause, two similar dot stimuli were presented simultaneously, the constant-numerosity reference on the right (at the same position as the adapter, and the variable test on the left), each for 500 ms. Participants judged which appeared to be more numerous (75 trials per condition), leading to psychometric curves, whose median gives the point of subjective equality (PSE: further details in supplemental material). **B.** Bars show the magnitude of the adaptation, expressed as the percentage difference in adaptation and baseline conditions. The dots on the bars show individual data, error bars ±1 s.e.m. **C.** Aggregate psychometric functions after adapting to a 6-dot stimulus and testing with a 12-dot stimulus (methods otherwise as described above). Here the adaptation effect was positive indicating an overestimation of the reference stimulus. **D.** Bar graph showing individual and average adaptation effects.

To evaluate the overall contribution of item adaptation it is necessary to consider it in context, comparing the *magnitude* of adaptation with and without dot overlap. Figure 3a shows psychometric functions for numerosity discrimination measured with robust psychophysical techniques under four critical conditions: baseline (unadapted); all test-dots overlap with adaptor-dots; no test- and adaptor-dots overlap; and test- and adaptor-dots both fully randomized (standard condition). All participants showed strong adaptation in all three adapting conditions (no need for statistics), with an average decrease in PSE of 17.5 dots, corresponding to an adaptation effect of 35% of the standard. That is more than 2 JNDs. Importantly, the three adaptation conditions were *indistinguishable* (Fig. 3b), irrespective of dot overlap (see demo 1²), with virtually none of the adaptation effect due to "item adaptation". Overlap may well have a slight effect on adaptation (especially when forward masking is permitted), but this tiny purported effect (about 1/5th of a JND) is dwarfed by the main adaptation effect of 2 JNDs. Whether "Item adaptation" exists or not, it does not even begin to explain *quantitatively* numerosity adaptation, which is surprisingly robust to the positioning of the adapting and test dots.

Yousif also acknowledge that reverse adaptation (adapt low, test medium) is strong evidence for numerosity adaptation. This effect was first reported by Burr and Ross (2008), and later replicated by Aagten-Murphy and Burr (2016, fig 2) with very brief adaptation stimuli. More recently, Aulet and Lourenco (2023) used very sophisticated techniques to show that adapting to 50 dots decreased the apparent numerosity of fields with fewer dots and increased that of fields with more dots, implicating multiple channels, rather than a simple gradient system). And as Figure 1a shows, Zimmermann (2018) demonstrated spatial selectivity of adaptation with both high and low adaptors. Here we measured reverse adaptation yet again, adapting to 6 dots and testing with a pattern of 12 dots (well within the *estimation* rather than *texture* ranges of numerosity: Anobile et al., 2014). Figures 3c,d show the results: the adaptation effect was robust, affecting all participants (again, no need for statistics), increasing perceived numerosity by 16% on average.

It is not obvious how to explain the discrepancy between our and Yousef et al's results, but one likely candidate is the density of the stimuli. Yousif et al used a dense field of 100 dots,

² demo1.mov

more a "texture" than a countable dot array (see their Fig. 3), whereas we deliberately chose sparse patterns to stay comfortably within the estimation range. As there is strong evidence that mechanisms for dense patterns are distinct from those to sparse patterns, following different psychophysical laws (Anobile et al., 2014; Anobile, Castaldi, et al., 2016; Anobile, Cicchini, et al., 2016; Burr et al., 2017; Pomè, Anobile, Cicchini, & Burr, 2019; Pomè, Anobile, Cicchini, Scabia, et al., 2019), this difference becomes relevant. Zimmerman (2018) also reported weaker reverse adaptation at higher densities (his Fig. 3c), consistent with the notion of different systems for number-estimation and texture-density. It would be interesting to explore this difference systematically: perhaps adaptation to low stimuli is specific to number rather than texture perception, further evidence for a specialized number system. But for the purposes of this discussion, we can confidently assert that when stimuli are well within the estimation range, reverse adaptation is strong and robust, increasing perceived numerosity by 16%, despite the absence of "old news".

Feature-specificity of number adaptation

Yousif et al refer to number adaptation is *brittle*, citing Grasso et al's (2022) report on the selectivity of numerosity adaptation: "changing the color of test displays as compared with the original adaptors *eliminated the number adaptation effect entirely*" (p6, their italics). We certainly agree that colour selectivity is surprising (and interesting), but *selectivity* does not equate with *brittleness*. Actually, changing the colour of the test does <u>not</u> *eliminate the number adaptation effect entirely* (see Fig. 2 of Grasso et al, and our Fig. 4), but it certainly reduces it considerably. This clearly speaks to the functional role of adaptation, as numerosity is specific to classes of items (such as ripe cherries, or predictors), not the total number of "things" out there, even if the mechanisms underlying this fascinating functional specificity remain obscure.

Since the original study, Caponi, Castaldi, Grasso and Arrighi (2024) have investigated whether the specificity is unique for colour, or may apply to other features, such as motion (a very salient feature), shape, faces, luminance and, again, colour. The results are summarized in Figure 4. As Grasso et al. (2022) reported, adaptation did not generalize completely across colour, but was reduced by a factor of three for non-congruent colours (from 27% to 10% adaptation). Nor did it generalize across luminance, although the effect was weaker, a factor of roughly 1.5. But adaptation did generalize completely for motion, letter-type and faces/non-faces. There were small congruency-dependent differences for shape and letter-case, which were statistically, but probably not functionally, significant. These studies show that adaptation is not always specific to feature type, as the "old news" hypothesis probably predicts, but that the generalization depends crucially on feature type, being strongest for colour.



Figure 4

Selectivity of numerosity adaptation. Participants adapted to 48 or 72 items (depending on condition) and were tested against a reference of 24 items. The adapting items were either the congruent or incongruent with the test, in colour, luminance, shape, letter-case, letter-type, motion or faces. *** p < 0.0001, * p < 0.05. Full experimental details in Caponi, Castaldi, Grasso, et al. (2024).

What is special about colour? Colour is a salient attribute, leading to "pop-out" (D'Zmura, 1991). It can be important for survival (such as signalling ripe fruit), and it is relatively invariant with viewpoint, shading, and distance. Motion, on the other hand, is not a fixed attribute of an object: a flock of birds can suddenly take to flight, or change direction. Halberda et al (2006) showed that human observers can enumerate in a single glance up to three intermingled sets of dots defined by their colour, with very little cost, showing that colour-defined dots make up a set which can be readily enumerated in parallel. It is not unreasonable that each colour-coded enumerable set can be adapted independently, even when spatially overlapping. It would be interesting to see if the number of items that can be enumerated in parallel predicts adaptation selectivity for the features reported in Figure 4, and for frequency of auditory tones.

The selective nature of visual numerosity adaptation, despite its susceptibility to cross-modal adaption, points to a highly functional mechanism, of great theoretical interest. Adaptation can be complex, as contingency aftereffects such as the McCulloch Effect (1965) show. Even basic, low-level features like orientation and colour show selective adaptation for *conjunctions* of features, where alternate adaptation to red vertical and green horizontal lines cause vertical white lines to appear green and horizontal lines red. The adaptation specificity for combinations of otherwise simple features is at least as surprising as partial colour-specificity of numerosity adaptation, and equally illusive to explanations by simple known mechanisms in early vision. It is interesting, and perhaps worth pursuing, that the most robust and well known of the contingency aftereffects involve colour.

How can numerosity adaptation be so selective for visual stimuli, yet generalise across sensory modality (and across space and time)? This is a fascinating question meriting much further research. However, it is by no means impossible, or even unreasonable: while adaptation is strongest for similarly coloured items, it remains highly significant (p < 0.001) for unmatched

colours, which reduce apparent numerosity by 10% (Fig. 4). The complex phenomenon of numerosity adaptation seems to comprise both selective and non-selective components, revealed by different experimental designs.

Incidentally, this series of experiments demonstrated another important fact. Although Yousif et al claim otherwise (p16), Caponi et al. (2024) reported clear and robust adaptation to moving stimuli, contrary to the predictions of the "old news" hypothesis: continually changing items are all "new news". If you are unsure whom to believe with all these contradictory claims, try out the demonstration³ for yourself: it is not a subtle effect.

Adaptation and the "old news" hypothesis

Adaptation is one of the most ubiquitous and extensively studied phenomena in neuroscience. It occurs at early levels of every sensory system, allowing us to see efficiently over a dynamic range of eight orders of magnitude, cope with noisy environments, and not be disturbed constantly by the taste of our saliva. It occurs for both low-level visual features such as colour and luminance, as well as higher-order features, such as face perception (Webster et al., 2004), biological motion (Karaminis et al., 2020) and even "causality" (Rolfs et al., 2013). If the *number sense* did not adapt it would be unique amongst perceptual attributes, worthy of very special attention.

Adaptation has been referred to as the psychophysicist's micro-electrode (Frisby, 1980) and studied by behavioural, physiological and biophysical techniques, in humans and animals (Clifford & Rhodes, 2005; Thompson & Burr, 2009; Webster, 2015). A range of computational models account for most features of adaptation (eg Heeger, 1992), and the cortical mechanisms have begun to be understood. For the simpler forms of adaptation (such as light adaptation), the mechanisms are understood at the level of membrane potentials, particularly calcium channels (Partridge & Stevens, 1976). Many theories have been advanced for the functional roles of adaptation, ranging from "cell fatigue", to maximizing the dynamic range for efficient neural coding (Barlow, 1990), acting as a homeostatic mechanism to equate and

³ Demo2.mov

maximize independence of neuronal responses (Benucci et al., 2013), to versions of predictive coding (Webster, 2011). Both neural fatigue and sharpening have been demonstrated by EEG decoding, with distinct timecourses (Rideaux et al., 2023). It is still not clear which purported function best describes number adaptation, but the "range" theories certainly seem relevant: Harvey and others (2013) have demonstrated clear neural coding for numerosity, which varies with the numerosity range of the stimuli. It is certainly feasible that adaptation could serve shift the range being encoded, maximizing the dynamic range of neuronal machinery (Barlow, 1990).

So how may the "old news" hypothesis fit in with (or supplant) the general scheme of adaptation? What mechanisms are being proposed, what psychophysical laws do they follow? None of this was considered in their review, but at first blush the predictive nature of "old news" would seem to relate to predictive coding and generative perception (see Cicchini et al., 2024 for review). These theories propose that perceptual systems *predict* what should be perceived, based (in part) on past experience, then verify the prediction against incoming data, signalling deviations from the predictions. After adaptation, the deviations would be large, and the signals perhaps exaggerated (consistent with well-known phenomena such as "mismatched negativity": Garrido et al., 2009). Pursuing this line of reasoning could well be profitable, but it should be clear that it is not in any way contrary to the more encompassing concept of *adaptation*, which must interact with other assimilative processes inherent in predictive models of perception (Taubert et al., 2016). Indeed, one may well question whether there is a real need for a new – and somewhat clumsy – term such as "old-news", when there already exists "predictive coding", "generative perception", "free energy" (Friston & Kiebel, 2009), and even Richard Gregory's (Gregory et al., 1997) quaint but enormously insightful idea of "hypothesis testing".

Conclusions

So, what should we conclude? "Is there hope for number adaptation?" (Yousif et al, p27). Or should we discard the concept – along with decades of research – in favour of the new "*old news*" hypothesis? Perhaps not. In the end, Science is quantitative: and following LaPlace

(1912), extraordinary claims ask for extraordinary evidence. Most of the evidence presented, epitomized by that supporting their pivotal claim of "item adaptation", strikes us as somewhat less than "*extraordinary*" (see Fig. 3 and demo 1²).

On the other hand, there exists overwhelming evidence for numerosity adaptation, from a diverse range of psychophysical, electrophysiological, magnetic resonance and pupillometry studies, none yet disproven or discredited. All the critical cases raised by Yousif et al. have held up to close scrutiny: reverse adaptation, cross-modal adaptation, and adaptation to dynamic stimuli have all been verified in many laboratories, and some again here (with two very clear demonstrations^{2,3}). Research into numerosity adaptation has gone well beyond simply confirming the existence of the phenomenon, by quantifying important properties such as perceptive field size, selectivity to colour or tone, and the site of action of the adaptation. Yousef et al's (p27) "strongest reason to doubt the existence of cross-modal adaptation" is that number adaptation is colour-selective. This seems to us as logical as using Celeste McCullough's (1965) classic demonstration of colour-contingent adaptation to challenge the existence of orientation adaptation: in fact, both examples reinforce the functional importance of adaptation mechanisms, rather than providing evidence against their existence.

So while we appreciate the efforts of Yousif et al to search for alternatives, it would seem premature to dispense with adaptation, which has proven invaluable for understanding so many basic, and also complex, perceptual phenomena. Nevertheless, we hope that their initiative may motivate new research, which could eventually lead to useful new concepts and understanding, in much the same way that the erroneous suggestion that numerosity perception was based on density judgments (Dakin et al., 2011; Durgin, 2008) led to the important discovery of separate density-dependent regimes for number and texture perception (Anobile, Cicchini, et al., 2016; Anobile et al., 2014).

Acknowledgments

Funded by the European Research Council (ERC: Grant Agreement No 832813-GenPercept) and European Union - Next Generation EU, in the context of The National Recovery and

Resilience Plan, Investment 1.5 Ecosystems of Innovation, Project Tuscany Health Ecosystem. (THE), CUP: B83C22003920001.

Data Availability

Original data published here are available at https://doi.org/10.5281/zenodo.11230370 (Burr et al., 2024).

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
- Anobile, G., Arrighi, R., Togoli, I., & Burr, D. C. (2016). A shared numerical representation for action and perception. *eLife*, *5*, e16161. https://doi.org/10.7554/eLife.16161
- Anobile, G., Castaldi, E., Turi, M., Tinelli, F., & Burr, D. C. (2016). Numerosity but not texturedensity discrimination correlates with math ability in children. *Developmental Psychology*, *52*(8), 1206–1216. https://doi.org/10.1037/dev0000155
- Anobile, G., Cicchini, G. M., & Burr, D. C. (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. C. (2016). Number As a Primary Perceptual Attribute: A Review. *Perception*, 45(1–2), 5–31. https://doi.org/10.1177/0301006615602599
- Anobile, G., Domenici, N., Togoli, I., Burr, D., & Arrighi, R. (2020). Distortions of visual time induced by motor adaptation. *Journal of Experimental Psychology. General*, *149*(7), 1333–1343. https://doi.org/10.1037/xge0000709

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

Aulet, L. S., & Lourenco, S. F. (2023). Visual adaptation reveals multichannel coding for numerosity. *Frontiers in Psychology*, *14*. https://doi.org/10.3389/fpsyg.2023.1125925

Barlow, H. B. (1990). A theory about the functional role and synaptic mechanism of visual aftereffects. In Blakemore, C., editor, Vision: Coding and Efficiency, 363-375. New York: Cambridge University Press.

- Benucci, A., Saleem, A. B., & Carandini, M. (2013). Adaptation maintains population homeostasis in primary visual cortex. *Nature Neuroscience*, *16*(6), 724–729. https://doi.org/10.1038/nn.3382
- Brooks, K. R., Clifford, C. W. G., Stevenson, R. J., Mond, J., & Stephen, I. D. (2018). The highlevel basis of body adaptation. *Royal Society Open Science*, 5(6), 172103. https://doi.org/10.1098/rsos.172103
- Burr, D. C., Anobile, G., & Arrighi, R. (2017). Psychophysical evidence for the number sense. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 373(1740), 20170045. https://doi.org/10.1098/rstb.2017.0045
- Burr, D. C., Arrighi, R., & Anobile, G. (2024). *Number adaptation: Reply [Data set]. Zenodo.* [dataset]. https://doi.org/10.5281/zenodo.11230370
- Burr, D. C., Cicchini, G. M., Arrighi, R., & Morrone, M. C. (2011). Spatiotopic selectivity of adaptation-based compression of event duration. *Journal of Vision*, 11(2), 21. https://doi.org/10.1167/11.2.21
- Burr, D. C., & Morrone, M. C. (2012). Constructing Stable Spatial Maps of the Word. *Perception*, 41(11), 1355–1372. https://doi.org/10.1068/p7392

- Burr, D. C., & 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. C., 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
- Caponi, C., Castaldi, E., Burr, D. C., & Binda, P. (2024). Adaptation to numerosity affects the pupillary light response. *Scientific Reports*, *14*, 6097. https://doi.org/10.1038/s41598-024-55646-w
- Caponi, C., Castaldi, E., Grasso, P., & Arrighi, R. (2024). *Feature selective adaptation of numerosity perception* (p. 2024.05.16.594539). bioRxiv. https://doi.org/10.1101/2024.05.16.594539
- 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., Pomè, A., Cicchini, G. M., Burr, D., & Binda, P. (2021). The pupil responds spontaneously to perceived numerosity. *Nature Communications*, *12*(1), 5944. https://doi.org/10.1038/s41467-021-26261-4
- Cicchini, G. M., Mikellidou, K., & Burr, D. C. (2024). Serial Dependence in Perception. Annual Review of Psychology, 75(Volume 75, 2024), 129–154.

https://doi.org/10.1146/annurev-psych-021523-104939

Clifford, C. W. G., & Rhodes, G. (Eds.). (2005). *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision*. Oxford University Press.

- Crespi, S., Biagi, L., d'Avossa, G., Burr, D. C., Tosetti, M., & Morrone, M. C. (2011). Spatiotopic Coding of BOLD Signal in Human Visual Cortex Depends on Spatial Attention. *PLOS ONE*, *6*(7), e21661. https://doi.org/10.1371/journal.pone.0021661
- d'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D. C., & Morrone, M. C. (2007). Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nature Neuroscience*, *10*(2), 249–255. https://doi.org/10.1038/nn1824
- 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

- Drissi-Daoudi, L., Öğmen, H., Herzog, M. H., & Cicchini, G. M. (2020). Object identity determines trans-saccadic integration. *Journal of Vision, 20*(7), 33. https://doi.org/10.1167/jov.20.7.33
- Duhamel, J.-R., Bremmer, F., Ben Hamed, S., & Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature*, *389*(6653), 845–848. https://doi.org/10.1038/39865
- 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

D'Zmura, M. (1991). Color in visual search. *Vision Research*, *31*(6), 951–966. https://doi.org/10.1016/0042-6989(91)90203-H

Fornaciai, M., & Park, J. (2017). Distinct Neural Signatures for Very Small and Very Large Numerosities. *Frontiers in Human Neuroscience*, *11*.

https://doi.org/10.3389/fnhum.2017.00021

Frisby, J. (1980). Seeing: Illusion, Brain, and Mind. Oxford University Press.

Friston, K., & Kiebel, S. (2009). Predictive coding under the free-energy principle. Philosophical Transactions of the Royal Society B: Biological Sciences, 364(1521), 1211–1221. https://doi.org/10.1098/rstb.2008.0300

- Gallagher, R. M., Suddendorf, T., & Arnold, D. H. (2019). Confidence as a diagnostic tool for perceptual aftereffects. *Scientific Reports*, *9*, 7124. https://doi.org/10.1038/s41598-019-43170-1
- Galletti, C., Battaglini, P. P., & Fattori, P. (1993). Parietal neurons encoding spatial locations in craniotopic coordinates. *Experimental Brain Research*, *96*(2), 221–229. https://doi.org/10.1007/BF00227102
- Garrido, M. I., Kilner, J. M., Stephan, K. E., & Friston, K. J. (2009). The mismatch negativity: A review of underlying mechanisms. *Clinical Neurophysiology*, *120*(3), 453–463. https://doi.org/10.1016/j.clinph.2008.11.029
- Grasso, P. A., Anobile, G., Arrighi, R., Burr, D. C., & Cicchini, G. M. (2022). Numerosity perception is tuned to salient environmental features. *iScience*, *25*(4), 104104. https://doi.org/10.1016/j.isci.2022.104104
- Grasso, P. A., Petrizzo, I., Caponi, C., Anobile, G., & Arrighi, R. (2022). Visual P2p component responds to perceived numerosity. *Frontiers in Human Neuroscience*, *16*. https://doi.org/10.3389/fnhum.2022.1014703
- Grasso, P. A., Petrizzo, I., Coniglio, F., & Arrighi, R. (2024). Electrophysiological correlates of temporal numerosity adaptation. *Frontiers in Neuroscience*, *18*, 1349540. https://doi.org/10.3389/fnins.2024.1349540
- Gregory, R. L., Longuet-Higgins, H. C., & Sutherland, N. S. (1997). Perceptions as hypotheses. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences,* 290(1038), 181–197. https://doi.org/10.1098/rstb.1980.0090

Halberda, J., Sires, S. F., & Feigenson, L. (2006). Multiple Spatially Overlapping Sets Can Be Enumerated in Parallel. *Psychological Science*, *17*(7), 572–576. https://doi.org/10.1111/j.1467-9280.2006.01746.x

- 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
- Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience*, *9*(2), 181–197. https://doi.org/10.1017/S0952523800009640
- Hyde, D. C., & Spelke, E. S. (2012). Spatiotemporal dynamics of processing nonsymbolic number: An event-related potential source localization study. *Human Brain Mapping*, 33(9), 2189–2203. https://doi.org/10.1002/hbm.21352
- Karaminis, T., Arrighi, R., Forth, G., Burr, D., & Pellicano, E. (2020). Adaptation to the Speed of Biological Motion in Autism. *Journal of Autism and Developmental Disorders*, *50*(2), 373–385. https://doi.org/10.1007/s10803-019-04241-4

LaPlace, P., Simon. (1812). Théorie analytique des Probabilités Suppl. Paris: Courcier.

Maldonado Moscoso, P. A., Cicchini, G. M., Arrighi, R., & Burr, D. C. (2020). Adaptation to hand-tapping affects sensory processing of numerosity directly: Evidence from reaction times and confidence. *Proceedings. Biological Sciences*, *287*(1927), 20200801. https://doi.org/10.1098/rspb.2020.0801

McCollough, C. (1965). Color Adaptation of Edge-Detectors in the Human Visual System. Science, 149(3688), 1115–1116. https://doi.org/10.1126/science.149.3688.1115

Mikellidou, K., Turi, M., & Burr, D. C. (2017). Spatiotopic coding during dynamic head tilt. Journal of Neurophysiology, 117(2), 808–817. https://doi.org/10.1152/jn.00508.2016 Partridge, L. D., & Stevens, C. F. (1976). A mechanism for spike frequency adaptation. *The Journal of Physiology*, 256(2), 315–332.

https://doi.org/10.1113/jphysiol.1976.sp011327

- Piazza, M., & Eger, E. (2016). Neural foundations and functional specificity of number representations. *Neuropsychologia*, *83*, 257–273. https://doi.org/10.1016/j.neuropsychologia.2015.09.025
- 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
- Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron*, 53(2), 293–305. https://doi.org/10.1016/j.neuron.2006.11.022
- 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. https://doi.org/10.1167/19.6.14
- Pomè, A., Anobile, G., Cicchini, G. M., Scabia, A., & Burr, D. C. (2019). Higher attentional costs for numerosity estimation at high densities. *Attention, Perception, & Psychophysics*, *81*(8), 2604–2611. https://doi.org/10.3758/s13414-019-01831-3

 Ranieri, G., Burr, D. C., Arrighi, R., & Grasso, P. A. (2023). *Investigating the neural correlates* of numerosity adaptation through EEG single-trial decoding. European Conference on Visual Perception, Paphos, Cyprus. https://journals.sagepub.com/pbassets/ecvp23_abstracts_UPD-1702301447867.pdf Rhodes, G., Evangelista, E., & Jeffery, L. (2009). Orientation-sensitivity of face identity aftereffects. *Vision Research*, *49*(19), 2379–2385. https://doi.org/10.1016/j.visres.2009.07.010

- Rideaux, R., West, R. K., Rangelov, D., & Mattingley, J. B. (2023). Distinct early and late neural mechanisms regulate feature-specific sensory adaptation in the human visual system. *Proceedings of the National Academy of Sciences*, *120*(6), e2216192120.
 https://doi.org/10.1073/pnas.2216192120
- Rolfs, M., Dambacher, M., & Cavanagh, P. (2013). Visual Adaptation of the Perception of Causality. *Current Biology*, 23(3), 250–254.

https://doi.org/10.1016/j.cub.2012.12.017

- Taubert, J., Alais, D., & Burr, D. (2016). Different coding strategies for the perception of stable and changeable facial attributes. *Scientific Reports*, 6(1), 32239. https://doi.org/10.1038/srep32239
- Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology*, *19*(1), R11–R14. https://doi.org/10.1016/j.cub.2008.10.014

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*, 713565. https://doi.org/10.3389/fnhum.2021.713565

Turi, M., & Burr, D. (2012). Spatiotopic perceptual maps in humans: Evidence from motion adaptation. *Proceedings of the Royal Society B: Biological Sciences*, 279(1740), 3091–3097. https://doi.org/10.1098/rspb.2012.0637

Webster, M. A. (2011). Adaptation and visual coding. Journal of Vision, 11(5), 3.

https://doi.org/10.1167/11.5.3

- Webster, M. A. (2015). Visual Adaptation. *Annual Review of Vision Science*, 1(Volume 1, 2015), 547–567. https://doi.org/10.1146/annurev-vision-082114-035509
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, *428*(6982), 557–561. https://doi.org/10.1038/nature02420
- Yang, H., Jia, L., Zhu, J., Zhang, J., Li, M., Li, C., & Pan, Y. (2024). The interplay of motor adaptation and groupitizing in numerosity perception: Insights from visual motion adaptation and proprioceptive motor adaptation. *PeerJ*, *12*, e16887.

https://doi.org/10.7717/peerj.16887

Yousif, S., Clarke, S., & Brannon, E. (2024). Number adaptation: A critical look.

Zimmermann, E. (2018). Small numbers are sensed directly, high numbers constructed from size and density. *Cognition*, *173*, 1–7.

https://doi.org/10.1016/j.cognition.2017.12.003