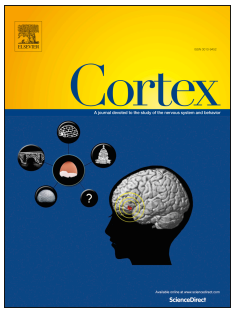
Journal Pre-proof



Tactile numerosity is coded in external space

Irene Togoli, Cathy Marlair, Olivier Collignon, Roberto Arrighi, Virginie Crollen

PII: S0010-9452(20)30389-0

DOI: https://doi.org/10.1016/j.cortex.2020.10.008

Reference: CORTEX 3063

To appear in: *Cortex*

Received Date: 12 June 2020

Revised Date: 13 September 2020

Accepted Date: 14 October 2020

Please cite this article as: Togoli I, Marlair C, Collignon O, Arrighi R, Crollen V, Tactile numerosity is coded in external space, *CORTEX*, https://doi.org/10.1016/j.cortex.2020.10.008.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2020 Published by Elsevier Ltd.

Journal Pre-proof

Tactile numerosity is coded in external space

Irene Togoli[1*], Cathy Marlair[2], Olivier Collignon[2], Roberto Arrighi[3*], Virginie Crollen[2]

[1]International School for Advanced Studies (SISSA), Trieste, Italy; [2]Psychological Sciences Research Institute (IPSY) and Institute of NeuroScience (IoNS), Université Catholique de Louvain, Louvain-la-Neuve, Belgium; 3. University of Florence, Department of Neuroscience, Psychology and Child Health, Florence, Italy

Journal Pre-proof

[*]**Corresponding author:** Irene Togoli, International School for Advanced Studies (SISSA), 34136, Trieste (TS), Italy; email irene.togoli@gmail.com. Roberto Arrighi, University of Florence, Department of Neuroscience, Psychology and Child Health, Florence, Italy; email roberto.arrighi@gmail.com

Journal Pre-proof

Abstract

Humans, and several non-human species, possess the ability to make approximate but reliable estimates of the number of objects around them. Alike other perceptual features, numerosity perception is susceptible to adaptation: exposure to a high number of items causes underestimation of the numerosity of a subsequent set of items, and vice versa. Several studies have investigated adaptation in the auditory and visual modality, whereby stimuli are preferentially encoded in an external coordinate system. As tactile stimuli are primarily coded in an internal (body-centered) reference frame, here we ask whether tactile numerosity adaptation operates based on internal or external spatial coordinates as it occurs in vision or audition. Twenty participants performed an adaptation task with their right hand located either in the right (uncrossed) or left (crossed) hemispace, in order for the two hands to occupy either two completely different positions, or the same position in space, respectively. Tactile adaptor and test stimuli were passively delivered either to the same (adapted) or different (non-adapted) hands. Our results show a clear signature of tactile numerosity adaptation aftereffects with a pattern of over- and under-estimation according to the adaptation rate (low and high, respectively). In the uncrossed position, we observed stronger adaptation effects when adaptor and test stimuli were delivered to the "adapted" hand. However, when both hands were aligned in the same spatial position (crossed condition), the magnitude of adaptation was similar irrespective of which hand received adaptor and test stimuli. These results demonstrate that numerosity information is automatically coded in external coordinates even in the tactile modality, suggesting that such a spatial reference frame is an intrinsic property of numerosity processing irrespective of the sensory modality.

Keywords: number sense, numerosity perception, adaptation, tactile perception, reference frame, spatial selectivity

Journal Pre-proof

1. Introduction

Humans, like many other animal species, are able to estimate numerosity. This ability, often referred to as the "*number sense*" (Hersh & Dehaene, 1998) is fundamental for survival as it allows for example to make rapid but suitable fight-or-flight choices (depending on the number of opponents), as well as to rapidly spot out regions with significant amounts of resources. Indeed, the human brain seems to be already equipped with an ability to roughly discriminate numerosity in infancy (de Hevia, Veggiotti, Streri, & Bonn, 2017; V. Izard, Sann, Spelke, & Streri, 2009; Lipton & Spelke, 2004), thus indicating an innate mechanism independent from linguistic or mathematical abilities (Barth, La Mont, Lipton, & Spelke, 2005; Cicchini, Anobile, & Burr, 2014; V. Izard et al., 2009).

Numerosity, like many primary visual properties (i.e., colour, size, distance, orientation) is susceptible to adaptation (e.g., see Kohn, 2007 for a review), a phenomenon whereby exposure to a given stimulus (adaptor) robustly affects the perception of the properties of a subsequent stimulus presented around the adapted region. For instance, exposure to a large quantity of items causes an underestimation of the numerosity of a subsequent set of items, while being exposed to a low numerosity causes overestimation (e.g., Burr & Ross, 2008). Numerosity adaptation – like other kinds of adaptation effects (e.g., rate adaptation; Levitan, Ban, Stiles, & Shimojo, 2015) – have been observed within different sensory modalities (i.e., vision, audition) and also to generalise across them (i.e., visual adaptation affecting auditory numerosity estimation, and vice versa; Arrighi, Togoli, & Burr, 2014). Moreover, this effect has also been shown to emerge independently from the format of the stimuli (i.e., simultaneously presented dot arrays vs. sequences of flashes; Arrighi et al., 2014), and even to be induced by a sequence of self-produced actions (Anobile, Arrighi, Togoli, & Burr, 2016; Anobile, Domenici, Togoli, Burr, & Arrighi, 2020).

Importantly, regardless of the kind of adaptation (sensory or motor) and the sensory modality of the stimuli (visual or auditory), adaptation aftereffects were found to be spatially selective in external, real-world, coordinates, with estimates being distorted just for stimuli presented around the adapted region. Moreover, in the case of motor adaptation or sensory adaptation for sequentially presented items, adaptation aftereffects were found to be coded in an external reference frame even in patients with a complete lack of visual experience (i.e., congenitally blind; Togoli, Crollen, Arrighi, & Collignon, 2020). These observations have led to the proposal that the native representational reference frame of numerosity is anchored to external space irrespective of the sensory modality tested.

However, in all aforesaid experiments, the sensory modality of the stimuli whose numerosity had to be estimated, was either visual or auditory, which are perceptual dimensions known to preferentially activate an external coordinate system (Heed, Buchholz, Engel, & Röder, 2015). It thus remains an open question whether such spatiotopic coding is a general property of numerosity processing, or a feature related to the sensory modalities investigated so far. Tactile stimulation, for instance, is primarily coded in an internal (skin-based) reference frame, before being automatically remapped into an external representation (Crollen, Albouy, Lepore, & Collignon, 2017; Heed et al., 2015; Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001). This raises the possibility that numerosity adaptation might show markedly different properties in the tactile modality.

The aim of the present study is therefore twofold: (1) obtaining a quantitative measure of numerosity adaptation in the tactile modality; (2) examining whether the tactile adaptation effect is selective in either a hand-centered or a spatiotopic reference frame. To address these questions, 20 participants were asked to perform a tactile numerosity estimation task after being adapted to either a low or high rate of tactile pulses. After delivering adaptation, the test stimulus (i.e., a sequence of tactile pulses) could be delivered to either the same hand that

received adaptation (*adapted* condition) or to the opposite hand (*non-adapted* condition). To assess the localization of the effect in internal or external coordinates, participants were positioned with both hands parallel to each other (i.e., right hand in the right hemispace, left hand in the left hemispace; *uncrossed* position) or with the right hand crossed over the body midline and aligned over the left hand (i.e., both hands in the same spatial position; *crossed* position). Our prediction is that adaptation should induce either under- or an over-estimation of tactile test stimulus numerosity, according to the adapting rate (i.e., high or low, respectively). In addition to that, we also predict that if tactile numerosity adaptation is coded according to an internal reference frame, it should remain confined to the adapted hand irrespective of its position. Alternatively, if adaptation is spatially selective in an external reference frame, it should affect test stimuli presented in the adapted location, irrespective of which hand receives them.

2. Methods

In this section, we report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. Participants

Twenty participants took part in the study. The group was composed of 9 males and 11 females with normal or corrected-to-normal vision and age varying between 18 and 51 years (M = 26, SD = 9.70). The inclusion criteria for participating in the study required the absence of any neurological, psychiatric, or developmental disorder. These inclusion criteria were established a priori before the start of the recruitment procedure. The participants were tested

individually and signed an informed consent form before participating in the study. Sixteen participants were right-handed, while the remaining four were left-handed. The procedures were approved by the Research Ethics Board of the Catholic University of Louvain (Belgium - Project 2016-26) and are in line with the Declaration of Helsinki. Note that the sample size was based on previous studies from our group investigating numerosity adaptation (Anobile et al., 2016; Togoli et al., 2020). Namely, we took the average effect size of the effect of adaptation across all the different conditions in which an effect of adaptation was predicted and observed in Anobile, Arrighi, et al. (2016) and Togoli et al. (2020). Doing so, we estimated an average effect size (Cohen's *d*) of 1.29. By assuming a two-tailed distribution and a power of 95%, we then estimated a minimum sample size of 10 participants. However, since the effect of numerosity adaptation in the tactile modality is unknown and it may differ in magnitude compared to previous experiments in different sensory modalities, we conservatively doubled such estimate by testing 20 participants. No participant was excluded from data analysis. The experimental and analytical procedures included in this work have not been preregistered.

2.2. Stimuli

The experiment was designed and executed using E-Prime (Psychology Software Tools, Inc.). The tactile stimulations were delivered using a pneumatic device driven by an air compressor. A membrane clipped by a plastic spring was placed on the first phalange of the middle finger and inflated with pulses of compressed air. The number of test stimuli varied between 16 and 20.

To minimize the temporal regularity of stimulation sequences, and to avoid a perceptual fusion of two or more consecutive stimuli (i.e., due to a too limited inter-stimulus interval; ISI), the ISI between any two consecutive tactile stimuli in each sequence was determined

randomly, with the constrain of a minimum ISI of 40 ms between two stimuli, a maximum ISI of 290 ms, and a maximum total sequence duration of 2 s.

2.3. Procedure

The experimental procedure consisted in two different phases: an adaptation phase and an estimation phase. In the adaptation phase, a sequence of tactile stimuli was delivered on either the right or the left hand during an interval of 6 seconds, and according to two adaptation conditions. In the "*high*" adaptation condition, the adapting stimulus rate was about 11-12 Hz, while in the "*low*" adaptation condition it was around 1-2 Hz. These two conditions were tested in two different blocks of trials. To avoid interactions between different adaptation conditions across different experimental blocks, the low adaptation stimuli were always delivered to the left hand, while the high adaptation stimuli to the right hand. The adaptation phase was announced by a recorded voice saying, in French: "*réception passive*" (passive reception). After adaptation, the estimation phase was announced by the same voice saying: "*estimation*" (estimation). In the estimation phase, either the right or the left hand was stimulated during an interval of 2 seconds (i.e., test stimulus; numerosity = 16, 17, 18, 19, or 20). We defined as "*adapted*" the trials in which the adaptor and test stimuli were delivered to the same hand (right or left, according to the adaptation condition), and as "*non-adapted*" the trials in which the adaptor and test stimuli were delivered on different hands (i.e., adaptation on right hand and test on the left hand, or vice versa - see Figure 1). At the end of the estimation phase, participants were asked to verbally report the number of stimuli they had perceived, and responses were collected by the experimenter. No feedback was provided regarding the participants' responses. Note that the different rates of adaptation used (i.e., 1 or 2 Hz for the low adaptation, and 11 or 12 Hz for the high adaptation), did not substantially modulate the adaptation effect. Hence, we collapsed the different rates together during data analysis (see *Supplementary Materials*, Fig. S2).

Journal Pre-proof

Before the experiment started, all participants were blindfolded and soundproof headphones were placed on the hears to avoid auditory feedback during the stimulation. Recorded message announcing the phases were delivered via external speakers and the volume was controlled so that the participant could still hear them despite the headphones.

To investigate the reference frame of the adaptation effect, participants were asked to perform the task under two postural conditions that were tested in separate blocks of trials. In the "*uncrossed*" condition, the left and right hand were located respectively in the left and right hemispace, 50 cm apart, with palms facing upward. In the "*crossed*" condition, the right hand was crossed over the body midline so that both the left and right hand were located in the same spatial position (vertical distance between the two hands around 5 cm - see Figure 1). If the spatial selectivity of adaptation is based on an internal reference frame, an adaptation effect should be observed only when the same hand is adapted and tested, regardless of where the hands are located. If the spatial selectivity of adaptation is instead based on an external reference frame, an adaptation effect should be found when the adaptor and test stimuli are delivered to the same spatial position, regardless of whether they are delivered to the same hand or opposite hands.

Journal Pre-proof

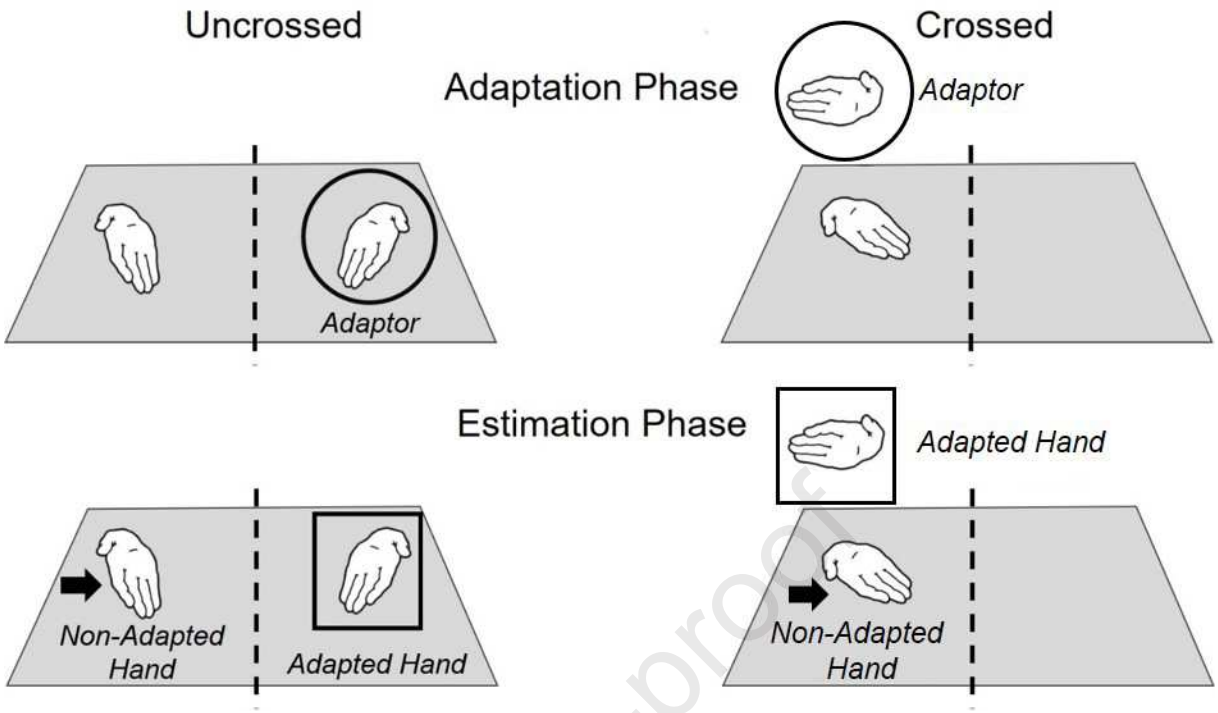


Figure 1. Illustration of the task's procedure. *Adaptation phase (upper panel) and estimation phase (lower panel). Participants performed the task in two postural conditions: uncrossed, with the left and right hands positioned respectively in the left and right hemispace (left panel); and crossed, with the left and right hand both positioned in the same position (right panel). The task also included two estimation conditions: adapted, where the same hand is adapted and tested; and non-adapted, where adaptation and test stimuli were delivered to different hands. Note that the example procedure depicted here refers to the low adaptation condition, in which the adaptor was delivered to the left hand; adapted and non-adapted hands were reversed in the high adaptation condition, in which the adaptor was delivered to the right hand.*

The two posture conditions (uncrossed vs. crossed) and the two adaptation conditions (high vs. low) were divided into four separate blocks of trials, with participants performing them in a random order. Each block was repeated twice and each numerosity (16, 17, 18, 19,

& 20) was presented 4 times for a total of 20 trials per block and 160 trials for the whole experiment, with an equivalent number of matched and unmatched trials. Note that the randomization of conditions was performed at the level of individual blocks, to avoid the systematic repetition of the same condition in immediately successive blocks and the potential build-up of adaptation that may result from it.

2.4.Statistical Analyses

For each participant, we calculated the average response for each numerosity in each experimental conditions (see Figure 2A). To assess the effect across different conditions, we used a three-way repeated measure ANOVA, with "posture" (uncrossed vs. crossed), "adaptation rate" (low vs. high), and "condition" (adapted vs. non-adapted) as factors. Since we did not observe any substantial difference in the adaptation effect across different numerosities (see *Supplementary Online Materials*), the different levels of numerosity were collapsed together during our main data analysis. To further assess the magnitude of the adaptation effect across different conditions, we computed an index of the adaptation effect (ΔEstimate) based on the difference between average numerical estimates after low and high adaptation:

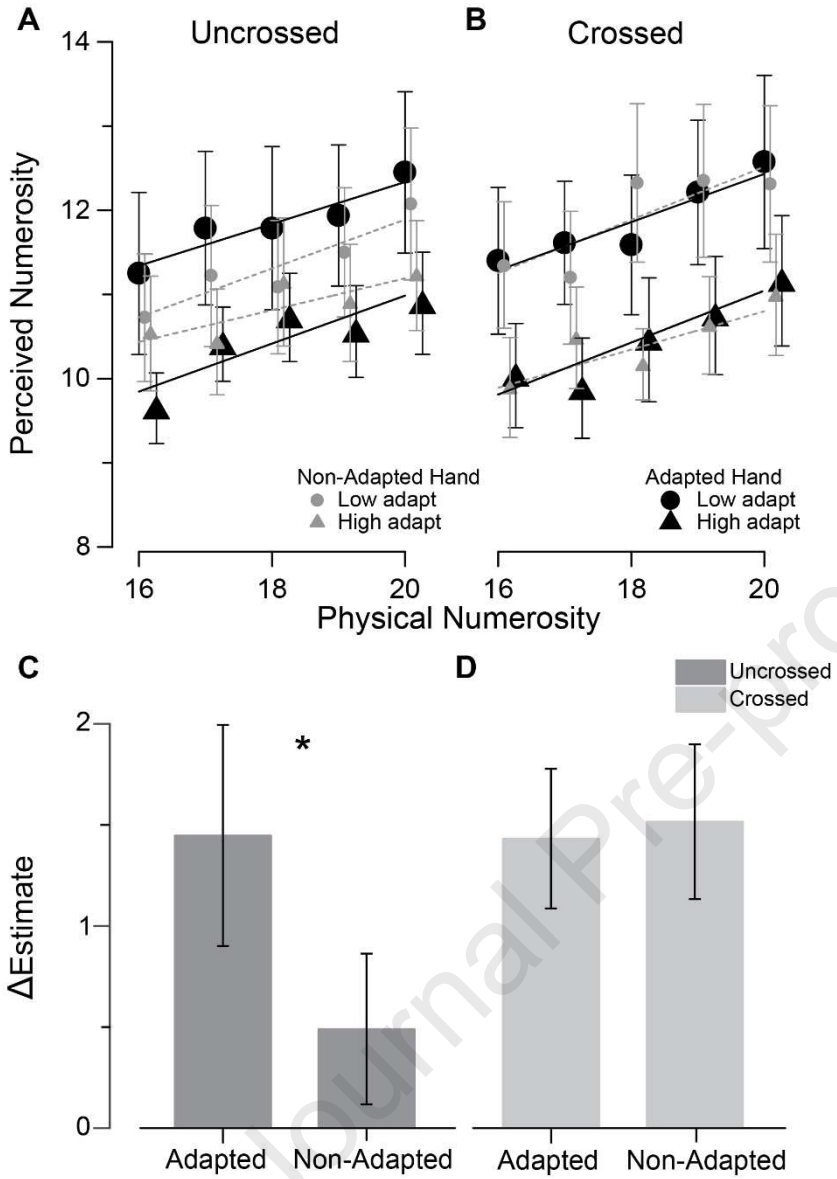
$$\Delta\text{Estimate} = \overline{PN_L} - \overline{PN_H};$$

where $\overline{PN_L}$ represents mean numerical estimates after low adaptation, and $\overline{PN_H}$ represents mean numerical estimates after high adaptation. In this context, a positive ΔEstimate value indicates an adaptation effect whereby low adaptation causes an overestimation of subsequent stimuli, and high adaptation causes underestimation. A negative value would instead reflect an opposite pattern compared to the expected effect of adaptation. ΔEstimate measures across participants and conditions were first tested individually with one-sample t-tests against the null hypothesis of zero difference. To account for multiple comparisons, we applied a false-

discovery rate (FDR) procedure, with q = 0.05. Then, we used a two-way repeated measures ANOVA with factor “posture” (uncrossed vs. crossed) and “condition” (adapted vs. non-adapted), followed up with a series of post-hoc t-tests. Also in this context, we adjusted the p-values with a FDR procedure (q = 0.05). Note that the effect of adaptation was computed as the difference between two adaptation conditions – and not for instance as the difference compared to a baseline condition – in order to avoid introducing biases due to the mere presence or absence of an additional stimulus in the sequence (i.e., the adaptor). Indeed, it is known that in the presence of multiple stimuli, their perception and judgments varies according to their order in the sequence (i.e., time-order error; see for instance Hellström, 1985). For this reason, we chose not to include a baseline, unadapted, condition and base the computation of the adaptation effect on the difference between two opposite adaptation conditions.

3. Results

Journal Pre-proof



225

226 ***Figure 2. Results.*** *(A-B) Effect of tactile adaptation on perceived numerosity in the uncrossed*
227 *(left panel) and crossed (right panel) positions. Mean responses for each numerosity*
228 *presented in the low (circle markers), and high (triangle markers) adaptation conditions.*
229 *Light-grey markers correspond to the "non-adapted" condition and black marker to the*
230 *"adapted" condition. Slant lines correspond to linear fits and error bars represent SEM.*
231 *Data points are shifted horizontally for the ease of visualization. (C-D) Adaptation effect*
232 *reported as the difference in average numerical estimates after low and high adaptation*

Journal Pre-proof

(ΔEstimate), for the adapted hand and non-adapted hand in both the uncrossed (dark grey) and crossed (light grey) postures. Error bars represent SEM.

Figure 2A and B show the pattern of adaptation effects observed in the different experimental conditions, for the full range of tested numerosities. As shown in the top panels of Figure 2 (A,B), when the adapting and the test stimuli were delivered to the same hand (dark symbols), regardless the posture (crossed or uncrossed) we observed a robust distortion of perceived numerosity, with the two adaptation conditions providing opposite effects (i.e., high adaptation induced underestimation and low adaptation overestimation). On the contrary, body posture strongly affected adaptation effects when test stimuli were delivered to the hand that had not been previously adapted. In the uncrossed condition (Fig. 2A), we did not find any substantial distortion induced by the two kinds of adaptation that generalized from the adapted to the non-adapted hand (grey symbols). However, in the crossed condition (B) – where participants positioned both hands in the same spatial position – the adaptation effects turned out to be virtually identical irrespective of which hand received adaptor and test stimuli. The distribution of individual PSE estimates across the different conditions is shown in Fig. S1 (see *Supplementary Online Materials*).

First, we carried out a 2 (posture: uncrossed vs. crossed) x 2 (adaptation rate: low vs. high) x 2 (condition: adapted vs. non-adapted) three-way repeated measures ANOVA on participants' mean estimations, averaged across all numerosities tested. The results showed a significant main effect of adaptation rate ($F(1,19) = 14.02$, $p = 0.001$, $\eta^2_p = 0.42$), no main effect of condition ($F(1,19) = 0.01$, $p = 0.92$), and no main effect of posture ($F(1,19) = 0.13$, $p = 0.72$; see Figure 2A). No two-way interaction was observed between pairs of factors (max $F = 4.20$, min $p = 0.054$).

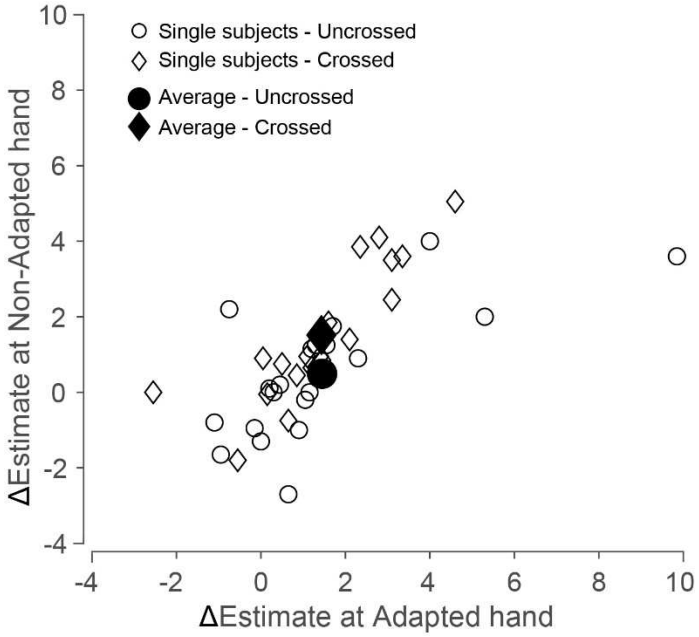


Figure 3. Individual adaptation effect estimates across the different condition. *The adaptation effect (ΔEstimate), computed as the difference between the PSE obtained in the low and high adaptation, is plotted as the effect measured when the test stimulus is delivered to the adapted hand (x-axis) versus when the test stimulus is delivered to the non-adapted hand (y-axis). Individual ΔEstimate values, in the uncrossed and crossed posture condition, are shown by the empty symbols (circles and diamonds, respectively). The bold filled symbols show the group average of the effect in the uncrossed and crossed condition (circle and diamond, respectively).*

More importantly, we observed a three-way interaction between posture, rate of adaptation, and condition ($F(1,19) = 5.57$, $p = 0.029$, $\eta^2_p = 0.23$). To better assess the nature of this interaction, we computed an index of the adaptation effect (ΔEstimate) based on the difference between numerical estimates obtained after low and high adaptation (Fig. 2C). We then used such ΔEstimate measures to compare the effect observed across the different conditions. To assess the effect of different adaptation conditions on average numerical estimates, we first performed a series of one-sample t-tests against the null hypothesis of zero

effect. Note that to account for multiple comparisons, p-values were adjusted using a FDR procedure with q = 0.05. In the uncrossed posture condition, the results show that the effect is significantly higher than zero in the adapted condition ($t(19) = 2.58$, adjusted-p = 0.024, Cohen's d = 0.57), while no significant effect was observed in the non-adapted condition ($t(19) = 1.28$, p = 0.22, d = 0.28). In the crossed condition, both effects in the adapted and non-adapted condition resulted to be significantly higher than zero ($t(19) = 4.04$, p = 0.002, d = 0.89, and $t(19) = 3.85$, p = 0.002, d = 0.86, respectively). Then, to assess the pattern of effects across the different conditions, we performed a two-way repeated measures ANOVA with factor "posture" (uncrossed vs. crossed) and "condition" (adapted vs. non-adapted). The results show no main effect of either posture ($F(1,19) = 1.31$, p = 0.27, $\eta_p^2 = 0.03$) or condition ($F(1,19) = 3.74$, p = 0.068, $\eta_p^2 = 0.05$), but a significant interaction between the two factors ($F(1,19) = 4.97$, p = 0.038, $\eta_p^2 = 0.22$). A series of post-hoc tests further showed that there is a significant difference between the adaptation effect obtained at the adapted and non-adapted hand in the uncrossed posture condition ($t(19) = 2.95$, FDR adjusted-p = 0.01, d = 0.43). On the other hand, no significant difference was instead observed in the crossed posture condition ($t(19) = 0.25$, p = 0.80, d = 0.05). The distribution of effects at the individual level is shown in Fig. 3.

4. Discussion

In the present study, we investigated the effect of tactile numerosity adaptation and its link to the representation of space. Previous studies concerning numerosity adaptation indeed observed a link between numerical and spatial processing, as demonstrated by the effect of adaptation being spatially localized according to external, real-world, coordinates (Anobile et

Journal Pre-proof

al., 2016; Arrighi et al., 2014; Togoli et al., 2020). However, previous studies in this context mostly focused on the visual and auditory modality, which are known to preferentially activate an external reference frame (Heed et al., 2015). Thus, it is unclear whether the spatial reference frame observed in numerosity adaptation actually reflects a native property of the numerosity processing system, or a property of the sensory modalities used to deliver information in previous studies.

To disentangle these two hypotheses, we used a tactile numerosity adaptation paradigm, with adaptation delivered either to the same hand as the test stimulus, or to a different hand. Crucially, participants positioned their hands either in a parallel posture in two completely different positions, or with one hand crossed over the body midline in order to be located in the same spatial position as the other. If the adaptation effect is coded in internal coordinates, then we should have observed an effect only when adaptor and test stimuli were delivered to the exact same hand. Conversely, if numerosity adaptation is coded in external coordinates, then the effect should have been observed when adaptor and test were delivered to the same spatial position, irrespective of the hand receiving them. Overall, our results clearly show that the adaptation effect is independent of which hand receives the adaptor stimulus, and it instead depends on the relative position of the hands in the external space.

Regarding the processing of tactile information, previous studies show that after an initial coding in an internal reference frame, tactile information is integrated with the current body posture. This process has been defined as tactile *remapping* and has been reported to occur in an external reference frame (Heed et al., 2015). Evidence for this remapping process in external coordinates notably comes from studies employing the temporal order judgment task (TOJ; Shore et al., 2002; Yamamoto & Kitazawa, 2001). In this task, in which participants were asked to judge the temporal order of two stimuli delivered to different hands, a decrease of performance was observed when participants perform the task with their

hands crossed over the body midline. Such an interference has been taken as evidence that different reference frames are automatically activated by tactile stimulation, leading to a crossing hand deficit when internal and external coordinates are mismatched.

While results obtained with a TOJ task show that task performance in that case is based on information remapped according to an external reference frame, little is known about tactile numerosity adaptation. Indeed, numerosity processing, especially in the visual modality, has been shown to involve multiple processing stages starting from very early sensory areas to higher-order associative areas (e.g., Cavdaroglu, Katz, & Knops, 2015; Fornaciai, Brannon, Woldorff, & Park, 2017; Fornaciai & Park, 2018; Park, DeWind, & Brannon, 2017; Roggeman, Santens, Fias, & Verguts, 2011). We thus had two predictions: if the reference frame of adaptation in this context depends on the reference frame preferentially activated by a specific sensory modality (i.e., external in vision and audition as tested in previous studies, internal in the tactile modality), then we should have observed adaptation in a body-centered reference frame. Alternatively, if numerosity is natively and intrinsically coded in an external reference frame, then we should have observed a spatial-based adaptation independent from the specific hand adapted.

Our results first show substantial numerosity adaptation effects in the tactile modality, extending previous findings on the generalized nature of the number sense and the processes affecting it. Second, this adaptation effect shows a clear selectivity for the position of the stimuli in an external reference frame. More specifically, when the hands were uncrossed, only the stimuli delivered on the adapted hand were influenced by adaptation. However, when both hands shared the same location, adaptation affected both the adapted and the non-adapted hand. These findings show that even in the tactile modality, numerosity adaptation operates in an external reference frame. Note that in our experimental design, the spatial separation of the hands in the uncrossed position was solely determined in the horizontal

dimension. Conversely, the vertical distance between the two hands in the crossed condition was determined in order for the two hands to be close enough for a spatially selective effect to be measurable. However, a question left open by adopting such design is whether it is sufficient to have the two hands within the same hemifield (irrespective, for instance, of the actual horizontal or vertical distance between the hands), or whether the adapted space is effectively limited to a three-dimensional space around the position of the adaptor stimulus. Our prediction is that such an effect would depend on both the horizontal and vertical distance between the position of the adaptor and adapted stimulus (i.e., the position of the two hands when the stimuli are delivered to different hands), irrespective of whether the hands occupy the same or different hemifield – as for instance visual adaptation depends on the relative coordinates and overlap between the stimuli on the screen (Ayhan, Bruno, Nishida, & Johnston, 2009). This in turn predicts that increasing the vertical distance between hands in the crossed condition should reduce the effect and make it to disappear with sufficiently large distance. Conversely, reducing the distance in the uncrossed condition might lead to observing a significant transfer of the adaptation effect across hands when they are sufficiently close to each other. However, our study was not designed to assess the extent of the "perceptual field" (e.g., see Anobile et al., 2020) determining the adaptation effect, but only to test its spatial specificity. Mapping the spatial extent and properties of the adapted field thus remains an interesting possibility for future studies.

Overall, this finding supports the idea that the native reference frame of numerosity processing is external. Indeed, converging evidence from previous research shows that such a spatial reference frame could be considered a default property of the numerosity encoding mechanism, emerging in a variety of different contexts. More specifically, numerosity adaptation effects not only similarly emerge in different modalities (i.e., visual and auditory as shown by previous studies, tactile as shown by the present work), but also cross-modally

(i.e., auditory numerosity adaptation affecting visual numerosity estimates, and vice versa), and across different presentation formats (i.e., sequences of events and arrays of spatially distributed items; see Arrighi et al., 2014).

Such a native coding in external coordinates might represent an emerging adaptive mechanism aimed to not only increase the efficiency of our perceptual representation of the external world, but also to optimize how we interact with it. Considering the multisensory nature of stimulation that we usually receive in naturalistic settings, the advantages of a unified reference frame are clear. For instance, having information from different sensory modalities coded in similar external coordinates provides the advantage of a more immediate coordination between perception and action in the service of goal-directed behaviour (i.e., programming a motor sequence to pick up a set of objects based on visual information, and adjusting it based on tactile feedback). In line with this idea, it has recently been demonstrated that perceived numerosity of both visual and auditory stimuli is susceptible of being distorted by the number of self-produced motor routines previously executed in the region of space the perceptual stimuli are presented in. In particular, it has been shown that fast tapping reduces the apparent numerosity of both temporal sequences and spatial arrays, while slow tapping yields an opposite effect, suggesting that the brain system processing numerosity encompasses shared mechanisms encoding the quantity of both internally and externally generated events (Anobile et al., 2016; Anobile et al., 2020).

Interestingly, the development of an external reference frame has been initially proposed to depend on the availability of early visual experience. Indeed, in early blind participants, crossing the hands does not affect performance when judging the temporal order of two stimuli, as opposed to sighted individuals who show an interference between the internal and external reference frames (Crollen et al., 2017; Röder, Rösler, & Spence, 2004). These results therefore suggest that the default use of an external frame of reference may

depend on early visual experience and that blind people preferentially use an anatomical coordinate system (Crollen et al., 2017; Röder et al., 2004). Recently, however, it has been demonstrated that visual experience is not a prerequisite for the development of an external coordinate system. A reference frame based on external coordinates has indeed been shown to be accessible to blind individuals when they must perform an action in the external world (Crollen et al., 2017; Heed & Röder, 2014) or when the instructions requires it (Crollen, Spruyt, Mahau, Bottini, & Collignon, 2019). While we show that tactile numerosity adaptation is coded in an external reference frame, a possibility raised by these previous observations is that such an effect may as well depend on the availability of early visual experience. In a recent study from our group, we have shown that, even in blind participants, the effect of adaptation on numerosity is coded in external coordinates, similarly to sighted individuals (Togoli et al., 2020). This therefore points to a fundamental link between numerosity and spatial processing that is even independent from visual experience, and may hence be rooted into the evolutionary history of this processing system. However, due to the different methodology used in our previous experiment (i.e., a motor adaptation procedure; Togoli et al., 2020) further evidence is needed to draw a stronger conclusion on this point.

Since our experimental design might resemble a vibrotactile "flutter" adaptation paradigm – which has been shown to affect perceptual magnitudes like time (Watanabe, Amemiya, Nishida, & Johnston, 2010) – a remaining question is whether the effect shown here could be entirely explained by tactile frequency adaptation. However, frequency adaptation has been shown to emerge very early in the tactile processing stream, at the level of the primary somatosensory cortex (S1; e.g., Romo & Salinas, 2003). Importantly, the information encoded by S1 neurons is largely limited to contralateral regions of the body (Harris, Harris, & Diamond, 2001; Harris, Miniussi, Harris, & Diamond, 2002; Shoham & Grinvald, 2001), and the effect of frequency adaptation should thus not transfer across

Journal Pre-proof

different hands. In contrast, our results show that the effect of adaptation in our paradigm could transfer from one hand to the other, provided that they occupy the same spatial position. This finding suggests that frequency adaptation per se could not be entirely responsible for the effect observed here, but that higher order mechanisms are most likely involved in this context. Tactile numerosity has been indeed shown to be encoded in a fronto-parietal brain network (Uluç, Velenosi, Schmidt, & Blankenburg, 2020), which may explain the ability of adaptation to transfer from one hand to the other. On the other hand, however, other interactions in tactile frequency perception seem to be modulated by the distance between the two hands (Rahman & Yau, 2019). For instance, Rahman & Yau (2019) demonstrated that frequency perception of a target vibrotactile stimulus delivered to one hand could be influenced by a distracter stimulus presented on the other hand, with the effect increasing as the distance between the two hands decreases. While this may appear to be very similar to our spatially-localized effect, the effect measured by Rahman & Yau (2019) is of very different nature (i.e., attractive effect, as opposed to the repulsive adaptation observed here), and could be explained by attention.

Thus, considering together previous (Anobile et al., 2016; Arrighi et al., 2014) and current results, all these findings point to the existence of a supra-modal, high-level mechanism encoding numerical information across multiple senses and across multiple presentation formats, in an abstract fashion. According to this view, while the numerosity processing pathway would start in early modality specific regions (e.g. DeWind, Park, Woldorff, & Brannon, 2019; Fornaciai et al., 2017; Fornaciai & Park, 2017, 2018; Roggeman et al., 2011; Van Rinsveld et al., 2020), information would later converge to higher-level associative areas (i.e., parietal cortex; e.g., Castaldi, Piazza, Dehaene, Vignaud, & Eger, 2019; Harvey, Klein, Petridou, & Dumoulin, 2013; Piazza, Mechelli, Price, & Butterworth, 2006) receiving signals from multiple sensory modalities (but see Cavdaroglu et al., 2015 and

Journal Pre-proof

Cavdaroglu & Knops, 2019 for results opposing to this idea). In this scenario, the coding in a common reference frame might be implemented at such a high-level, supra-modal, processing stage. However, considering the large difference in the paradigms used in the present and previous studies (Anobile et al., 2016; Arrighi et al., 2014), whether the spatial selectivity observed in different contexts reflects the same coding mechanism remains speculative. Further tests employing similar paradigms across different modalities are thus needed to address this possibility.

Finally, another point worth considering is the fact that the adaptation effects shown here are embedded in a pattern of systematic underestimation of numerosity. However, the underestimation of relatively high numerosities is not unusual, and largely in line with previous work (Crollen, Castronovo, & Seron, 2011; Izard & Dehaene, 2008). Such an underestimation might be due to the increasing logarithmic-like compression of numerical estimates usually observed in numerosity estimation tasks at relatively high numerical values (Cicchini et al., 2014; Fornaciai & Park, 2020). On the other hand, time-order errors (Hellström, 1985) could contribute to such systematic bias, inducing an underestimation due to the mere fact that our test stimuli were always presented after the adaptor stimulus.

5. Conclusion

To conclude, our results show for the first time that even in the tactile modality numerosity adaptation is spatially-localized in external coordinates. This finding further advances our understanding of numerosity perception by showing that the link between numerical and spatial processing extends beyond sensory modalities naturally favoring a spatial coding of the stimuli (i.e., vision and audition). We show that such a link exists even in a modality favoring an internal, body-centered reference frame, suggesting that the native

reference frame of numerosity processing is spatiotopic. This in turn points to the involvement of a genuinely supra-modal mechanism mediating numerosity representation and the adaptation effect. Overall, our results thus support the idea of an abstract and generalized number sense that gives humans and animals the ability to rapidly and correctly estimate quantities of items – an ability essential for survival.

Data availability: experimental/analytical materials and data relative to the experiments described in this manuscript are available on Open Science Framework following this link: https://osf.io/273vt/

Acknowledgement: We thank Dr. Michele Fornaciai for useful comments on an earlier version of this manuscript. This work was supported by a European Research Council starting grant (MADVIS grant #337573) and the Belgian Excellence of Science program from the FWO and FRS-FNRS (Project: 30991544) attributed to OC; by the Italian Ministry of Education, University, and Research PRIN2017 programme, Grant numbers 2017XBJN4F; and by the European Union's Horizon 2020 research and innovation programme ERC Advanced Grant number 832813 (GenPercept). OC is a research associate at the Fond National de Recherche Scientifique de Belgique (FRS-FNRS).

References

1. Anobile, G., Arrighi, R., Togoli, I. & Burr, D. C. A shared numerical representation for action and perception. Elife 5, (2016).

2. Anobile, G., Domenici, N., Togoli, I., Burr, D. & Arrighi, R. Distortions of visual time induced by motor adaptation. J. Exp. Psychol. Gen. 149, 1333–1343 (2020).

3. Arrighi, R., Togoli, I. & Burr, D. C. A generalized sense of number. Proc. R. Soc. B Biol. Sci. 281, 20141791 (2014).

4. Ayhan, I., Bruno, A., Nishida, S. & Johnston, A. The spatial tuning of adaptation-based time compression. J. Vis. 9, 2–2 (2009).

5. Barth, H., La Mont, K., Lipton, J. & Spelke, E. S. Abstract number and arithmetic in preschool children. Proc. Natl. Acad. Sci. 102, 14116–14121 (2005).

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

7. Cavdaroglu, S., Katz, C. & Knops, A. Dissociating estimation from comparison and response eliminates parietal involvement in sequential numerosity perception. Neuroimage 116, 135–148 (2015).

8. Cavdaroglu, S. & Knops, A. Evidence for a Posterior Parietal Cortex Contribution to Spatial but not Temporal Numerosity Perception. Cereb. Cortex 29, 2965–2977 (2019).

9. Cicchini, G. M., Anobile, G. & Burr, D. C. Compressive mapping of number to space reflects dynamic encoding mechanisms, not static logarithmic transform. Proc. Natl. Acad. Sci. 111, 7867–7872 (2014).

10. Crollen, V., Albouy, G., Lepore, F. & Collignon, O. How visual experience impacts the internal and external spatial mapping of sensorimotor functions. Sci. Rep. 7, 1022 (2017).

11. Crollen, V., Castronovo, J. & Seron, X. Under- and Over-Estimation. Exp. Psychol. 58, 39–49 (2011).

12. Crollen, V., Spruyt, T., Mahau, P., Bottini, R. & Collignon, O. How visual experience and task context modulate the use of internal and external spatial coordinate for perception and action. J. Exp. Psychol. Hum. Percept. Perform. 45, 354–362 (2019).

13. de Hevia, M. D., Veggiotti, L., Streri, A. & Bonn, C. D. At Birth, Humans Associate "Few" with Left and "Many" with Right. Curr. Biol. 27, 3879-3884.e2 (2017).

14. DeWind, N. K., Park, J., Woldorff, M. G. & Brannon, E. M. Numerical encoding in early visual cortex. Cortex (2019) doi:10.1016/j.cortex.2018.03.027.

15. Fornaciai, M., Brannon, E. M., Woldorff, M. G. & Park, J. Numerosity processing in early visual cortex. Neuroimage 157, 429–438 (2017).

16. Fornaciai, M. & Park, J. Spatiotemporal feature integration shapes approximate numerical processing. J. Vis. 17, 6 (2017).

17. Fornaciai, M. & Park, J. Early Numerosity Encoding in Visual Cortex Is Not Sufficient for the Representation of Numerical Magnitude. J. Cogn. Neurosci. 30, 1788–1802 (2018).

18. Fornaciai, M. & Park, J. Attractive serial dependence between memorized stimuli. Cognition 200, 104250 (2020).

19. Harris, J. A., Harris, I. M. & Diamond, M. E. The Topography of Tactile Working Memory. J. Neurosci. 21, 8262–8269 (2001).

Journal Pre-proof

20. Harris, J. A., Miniussi, C., Harris, I. M. & Diamond, M. E. Transient Storage of a Tactile Memory Trace in Primary Somatosensory Cortex. J. Neurosci. 22, 8720–8725 (2002).

21. Harvey, B. M., Klein, B. P., Petridou, N. & Dumoulin, S. O. Topographic Representation of Numerosity in the Human Parietal Cortex. Science (80-.). 341, 1123–1126 (2013).

22. Heed, T., Buchholz, V. N., Engel, A. K. & Röder, B. Tactile remapping: from coordinate transformation to integration in sensorimotor processing. Trends Cogn. Sci. 19, 251–258 (2015).

23. Heed, T. & Röder, B. Motor coordination uses external spatial coordinates independent of developmental vision. Cognition 132, 1–15 (2014).

24. Hellström, Å. The time-order error and its relatives: Mirrors of cognitive processes in comparing. Psychol. Bull. 97, 35–61 (1985).

25. Hersh, R. & Dehaene, S. The Number Sense: How the Mind Creates Mathematics. Am. Math. Mon. 105, 975 (1998).

26. Izard, V., Sann, C., Spelke, E. S. & Streri, A. Newborn infants perceive abstract numbers. Proc. Natl. Acad. Sci. 106, 10382–10385 (2009).

27. Izard, V. & Dehaene, S. Calibrating the mental number line. Cognition 106, 1221–1247 (2008).

28. Kohn, A. Visual Adaptation: Physiology, Mechanisms, and Functional Benefits. J. Neurophysiol. 97, 3155–3164 (2007).

29. Levitan, C. A., Ban, Y.-H. A., Stiles, N. R. B. & Shimojo, S. Rate perception adapts across the senses: evidence for a unified timing mechanism. Sci. Rep. 5, 8857 (2015).

30. Lipton, J. S. & Spelke, E. S. Discrimination of Large and Small Numerosities by Human Infants. Infancy 5, 271–290 (2004).

31. Park, J., DeWind, N. K. & Brannon, E. M. Direct and rapid encoding of numerosity in the visual stream. Behav. Brain Sci. 40, e185 (2017).

32. Rahman, M. S. & Yau, J. M. Somatosensory interactions reveal feature-dependent computations. J. Neurophysiol. 122, 5–21 (2019).

33. Röder, B., Rösler, F. & Spence, C. Early Vision Impairs Tactile Perception in the Blind. Curr. Biol. 14, 121–124 (2004).

34. Roggeman, C., Santens, S., Fias, W. & Verguts, T. Stages of Nonsymbolic Number Processing in Occipitoparietal Cortex Disentangled by fMRI Adaptation. J. Neurosci. 31, 7168–7173 (2011).

35. Romo, R. & Salinas, E. Flutter Discrimination: neural codes, perception, memory and decision making. Nat. Rev. Neurosci. 4, 203–218 (2003).

571 36. Shoham, D. & Grinvald, A. The Cortical Representation of the Hand in Macaque and
572 Human Area S-I: High Resolution Optical Imaging. J. Neurosci. 21, 6820–6835 (2001).

573 37. Shore, D. I., Spry, E. & Spence, C. Confusing the mind by crossing the hands. Cogn.
574 Brain Res. 14, 153–163 (2002).

575 38. Togoli, I., Crollen, V., Arrighi, R. & Collignon, O. The shared numerical representation
576 for action and perception develops independently from vision. Cortex (2020)
577 doi:10.1016/j.cortex.2020.05.004.

578 39. Uluç, I., Velenosi, L. A., Schmidt, T. T. & Blankenburg, F. Parametric representation of
579 tactile numerosity in working memory. eNeuro (2020) doi:10.1523/ENEURO.0090-
580 19.2019.

581 40. Van Rinsveld, A. et al. The neural signature of numerosity by separating numerical and
582 continuous magnitude extraction in visual cortex with frequency-tagged EEG. Proc. Natl.
583 Acad. Sci. 117, 5726–5732 (2020).

584 41. Watanabe, J., Amemiya, T., Nishida, S. & Johnston, A. Tactile duration compression by
585 vibrotactile adaptation. Neuroreport 21, 856–860 (2010).

586 42. Yamamoto, S. & Kitazawa, S. Reversal of subjective temporal order due to arm crossing.
587 Nat. Neurosci. 4, 759–765 (2001).

Journal Pre-proof

Journal Pre-proof

CRediT author statement

Conceptualization	IT, VC, RA, OC
Methodology	IT, VC, CM
Software	IT, VC
Formal analysis	IT, VC, CM, RA, OC
Investigation	IT, CM
Data Curation	IT, CM
Writing - Original Draft	IT, CM
Writing - Review & Editing	IT, CM, VC, RA, OC
Visualization	IT, CM
Supervision	RA, OC, VC
Project administration	IT, VC
Funding acquisition	RA, OC

Journal Pre-proof