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# **Adaptation to hand-tapping affects sensory processing of numerosity directly: evidence from reaction times and confidence**

Paula A. Maldonado Moscoso<sup>1</sup>, Guido M. Cicchini<sup>2</sup>, Roberto Arrighi<sup>1</sup> &  
David C. Burr<sup>1,2\*</sup>

1. Department of Neuroscience, Psychology, Pharmacology and Child Health, University of Florence, Florence, Italy
2. Institute of Neuroscience, National Research Council, Pisa, Italy

**\*Corresponding author:**

David. C. Burr  
davidcharles.burr@unifi.it

## **Abstract**

Like most perceptual attributes, the perception of numerosity is susceptible to adaptation, both to prolonged viewing of spatial arrays and to repeated motor actions such as hand-tapping. However, the possibility has been raised that adaptation may reflect response biases rather than modification of sensory processing. To disentangle these two possibilities, we studied visual and motor adaptation of numerosity perception while measuring confidence and reaction-times. Both sensory and motor adaptation robustly distorted numerosity estimates, and these shifts in perceived numerosity were accompanied by similar shifts in confidence and reaction-time distributions. After adaptation, maximum uncertainty and slowest response-times occurred at the point of subjective (rather than physical) equality of the matching task, suggesting that adaptation acts directly on the sensory representation of numerosity, before the decisional processes. On the other hand, making reward response-contingent, which also caused robust shifts in the psychometric function, caused no significant shifts in confidence or reaction-time distributions. These results reinforce evidence for shared mechanisms that encode the quantity of both internally and externally generated events, and advance a useful general technique to test whether contextual effects like adaptation and serial dependence really affect sensory processing.

**Keywords:** numerosity perception, adaptation, confidence, reaction-times, decision making.

# 1    **Introduction**

2    Perceptual adaptation is a form of short-term plasticity, usually generated by observing  
3    for some time a particular stimulus, such as a steadily drifting pattern. Adaptation has  
4    proven to be a fundamental psychophysical tool to study many perceptual properties,  
5    including high-level properties such as face identity and expression [1–3]. It has also  
6    proven invaluable in the study of the perception of *numerosity*, bringing this field of  
7    cognitive research into the realm of perceptual research [4–6]. Recently, cross-modal  
8    and cross-format adaptation have been used to demonstrate a “generalized sense of  
9    number”, showing strong interactions between the numerosities of spatial arrays of  
10    objects and temporal sequences of events [7]. Even more intriguingly, the authors went  
11    on to show interactions between numerosity perception and motor action: fast tapping  
12    reduces the apparent numerosity of both temporal sequences and spatial arrays, while  
13    slow tapping has the opposite effect [8].

14        These results are clearly important as they point to specific neural interactions  
15    between different forms of numerosity representation, reinforcing the  
16    neurophysiological evidence reported in macaque monkeys [9]. They also show strong  
17    neural links between numerosity and motor action, again with parallels in the  
18    neurophysiological literature [10]. But do adaptation studies truly reveal underlying  
19    neural mechanisms as Mollon [1] claimed (“if you can adapt it it’s there”)? Can we  
20    think of adaptation as the “psychologists microelectrode”, as suggested by Frisby [11]?

21    It has recently been questioned whether adaptation necessary reveals underlying neural  
22    mechanisms, with suggestions that they could result from changes in observer criteria,  
23    driven by cognitive, decisional processes, particularly for certain “high-level”  
24    aftereffects [for discussion see 12]. To demonstrate this possibility, Morgan et al. [13]  
25    showed that observers could simulate the effects of adaptation by adopting simple  
26    decision rules, along the lines of “if unsure say fewer”. This strategy resulted in a clear  
27    shift of psychometric functions, without broadening the width of the functions  
28    (reflecting preserved precision). Therefore, it is possible that in the numerosity  
29    adaptation experiments the changes in the psychometric functions do not reflect

30 changes in neural representations of number, but in a cognitive, decision strategy in  
31 reporting numerosity. Possibly after rapid tapping there is a tendency to report  
32 uncertain numerosities as low, and after slow tapping to report these as high. This could  
33 conceivably account for the changes in apparent numerosity, without invoking the  
34 action on neural mechanisms.

35 Morgan et al.'s idea can be illustrated with a simple simulation shown in  
36 Figure 1. The red curve illustrates a typical psychometric function, modelled by a  
37 cumulative Gaussian error function. The blue curve illustrates a hypothetical function  
38 of subjective confidence, based on the consistency of participant responses: one when  
39 certain, zero when guessing. On the basis of data from this study (see Figure 3) we  
40 assume minimal confidence is 50%, but this is not essential to the demonstration.  
41 Confidence should be minimal at the point of subjective equality, where sensory  
42 information is least. The green curve is the simulation of the strategy "if unsure say  
43 'fewer'" (the product of the two probability functions), causing a downward shift of  
44 the curve, which necessarily shifts the function rightwards. The downward shift in the  
45 curve is virtually indistinguishable from a rightward shift caused by sensory adaptation  
46 to numerosity. However, if it is confidence that drives the downward shift, the  
47 confidence function itself should not change, but remain centred at the PSE of the  
48 unadapted function.

49

50 ----- FIGURE 1 -----

51

52 Gallagher and colleagues [14] took advantage of this fact to propose a novel way  
53 of distinguishing between sensory effects in adaptation and higher-level decisional  
54 biases, based on the assumption that confidence in the perceptual decision will scale  
55 with the strength of sensory evidence. In the typical two-alternative matching  
56 experiment used to measure adaptation, where participants choose which of two stimuli  
57 was the largest, the strength of sensory evidence will be weakest when their internal

58 representations of magnitude are the same: that is, at the point of subjective equality  
59 (PSE). Therefore, the PSE should also correspond to the point of minimal confidence.  
60 If the PSE shifts with adaptation-induced changes in internal representations of  
61 magnitude, the shift in PSE should be accompanied by a comparable shift in minimal  
62 confidence. If, on the other hand, the adaptation results from weak confidence and a  
63 decision rule (as simulated in Figure 1), the confidence ratings should remain minimal  
64 at the point of physical equality, and not shift with adaptation. Gallagher et al. [14]  
65 showed that adaptation to visual motion shifted not only the point of perceived equality  
66 of motion, but also the point of maximal decisional uncertainty. On the other hand,  
67 instructing participants to introduce a systematic response bias (along the lines of  
68 replicating Morgan et al.'s experiment) did not shift the point of maximal uncertainty.

69 Another common tool in sensory research is reaction-times, which also vary  
70 systematically with sensory strength, well approximated by a power function of the  
71 stimulus strength plus a constant [Piéron's law: 15]. Following the same logic  
72 discussed above, reaction-times should also vary on a two alternative forced choice  
73 task, being maximal when the sensory representations of the two are most similar, at  
74 the point of subjective equality. Therefore, adaptation should also shift the peak in  
75 reaction-times, following the shift in PSE, if the effects are sensorial rather than  
76 decisional. If they remain anchored at physical equality, the adaptation is more likely  
77 to reflect response or decision biases.

78 In this study we investigate how adaptation to numerosity affects confidence  
79 ratings and reaction-times. We study two types of adaptation: visual adaptation to  
80 dense dot arrays [4], and motor adaptation to fast and slow hand-tapping [8]. The  
81 results show that both types of adaptation cause concomitant changes in both minimal  
82 confidence and maximal reaction-times, suggesting that the effects of both adaptation  
83 to high-numerosity and to manual tapping are sensory rather than biases in decision.

## 84    **Methods**

85    Stimuli were presented on an Acer LCD monitor (screen resolution of 1920 X 1080,  
86    refresh rate 60 Hz) subtending 50° X 29° at the subject view distance of 57 cm. They  
87    were created with PsychToolbox routines for MATLAB (ver. R2016a, the Mathworks,  
88    Inc.) on a PC computer running Windows 7. In the motor adaptation conditions, hand  
89    movements were monitored by an infrared motion sensor device (Leap motion  
90    controller – <https://www.leapmotion.com>) running at 60 Hz.

91            We used a standard forced-choice paradigm (Figure 2). Stimuli were brief  
92    (250 ms) patches of dots, presented sequentially to the left and right of fixation, with a  
93    200 ms pause between them. Each patch covered a circular region of 8° in diameter,  
94    centred at 7° from screen centre. Dots were 0.3° diameter, separated from each other  
95    by at least 0.25°, half white and half black (to balance luminance), presented on a grey  
96    background. The patch to the left of fixation was the reference, with numerosity fixed  
97    at 16 dots; that to the right was the probe, with numerosity varying randomly from 8 to  
98    32 dots (numerosity drawn from linear rectangle distribution). Participants first judged  
99    whether the stimulus on the left or the right appeared more numerous, then indicated  
100    their confidence in the judgments by pressing the up or down arrow (low or high  
101    confidence respectively). We also measured the reaction-times of the numerosity  
102    judgments, and report the mean, after removing outliers (more  $\pm 3$  standard deviations  
103    from the mean).

104

### 105    *Adaptation*

106    For the visual adaptation experiment, 12 participants (11 naïve to the purpose of the  
107    study and 1 author; mean age 28 with normal or corrected-to-normal vision) adapted  
108    to an array of 60 dots (adapt to high) at the same position as the probe stimulus, for 40  
109    s at the beginning of each session, then for 6 s top-up periods. Stimuli were presented  
110    1 s after adaptation. Each participant performed a total of 432 trials. For the adaptation-  
111    to-tapping experiment, participants (9 naïve to the purpose of the study and 1 author;

mean age 28 with normal or corrected-to-normal vision) made a series of hand-tapping movements (pivoting at the wrist) on the right side of the screen until a white central fixation point turned red (the stop signal); 1 s later the stimuli were presented. In one condition participants tapped as rapidly as possible, in another at around 1 Hz. The program continuously monitored tapping via the infrared motion sensor: if a tap occurred after the presentation of the test stimulus, the trial would be aborted. After the stimuli presentation, subjects were required to press left arrow when the stimulus at left was perceived as more numerous, or right arrow when the righthand stimulus was perceived as more numerous. They then pressed up-arrow if they were confident about the numerosity response or down-arrow if they were not. Participants were unaware that we also measured the reaction-time of the numerosity response, and they were not explicitly asked to make speeded responses. Three blocks of 24 trials were run for each condition.

125

126

### 127 *Manipulation of rewards*

128 We devised a control experiment to compare with adaptation, where we manipulated  
129 the reward rules. 10 adults participated in this study, 9 naïve to the purpose of the study  
130 (mean age 28 with normal or corrected-to-normal vision). Here there was no  
131 adaptation, but participants played a point-based game, with three types of reward  
132 regimes (in different blocks). In baseline blocks, they received 1 point for each correct  
133 response and lost 1 for every error (performing on average at 85% correct). In “reward-  
134 low” blocks, they received 2 points for correctly responded “less than”, and lost 1 for  
135 each error; and in “reward-high”, 2 points for correctly responding “greater than”,  
136 losing 1 for an error. They also indicated by pressing up-arrow if they were confident  
137 about the numerosity indicated was “less” or “greater than” or down arrow if they were  
138 not. They were given feedback on earning 50 points, and again at 80 points. Three  
139 blocks with at least 79 trials were run for each condition. We also measured the



140 reaction-time of the response, and again participants were not explicitly asked to make  
141 speeded responses.

142

### 143 *Data Analysis*

144 The proportion of trials where the test appeared more numerous than the probe was  
145 plotted against physical numerosity and fitted with cumulative Gaussian error  
146 functions. The median of the error functions estimates the point of subjective equality  
147 (PSE), and the difference in numerosity between the 50% and the 75% points gives the  
148 just notable difference (JND). The distributions of average confidence responses (1 for  
149 high, 0 for low) and of the mean of reaction-times were fitted with Gaussian  
150 distributions, and the peak of the fitted functions was taken as the point of maximum  
151 uncertainty or reaction-times.

$$152 \quad P(N) = b + a \cdot \exp\left(\frac{-(\bar{N}-N)^2}{2\sigma^2}\right) \quad \text{eqn. 2}$$

153 Where  $N$  is numerosity,  $P(N)$  the proportion of confident responses – or the  
154 average reaction-time – at that numerosity,  $b$  and  $a$  constants,  $\bar{N}$  the mean of the  
155 Gaussian and  $\sigma$  the standard deviation. When fitting data pooled over participants, all  
156 parameters were free to vary. When fitting individual participant data,  $b$  and  $\sigma$  were  
157 fixed to the values obtained for the aggregate data.

158 All analyses were performed both on the “aggregate participant”, pooling all data  
159 from all participants, and also on individual participant data. Significance of the  
160 aggregate data was calculated by bootstrap sign test: 10,000 reiterations, with  
161 replacement.

162 Experimental procedures were approved by the local ethics committee  
163 (*Comitato Etico Pediatrico Regionale Azienda Ospedaliero-Universitaria Meyer,*  
164 *Florence, Italy; protocol n. GR- 2013-02358262)* and are in line with the declaration  
165 of Helsinki. All subjects gave written informed consent.

166

## Results

### *Effects of adaptation on confidence and reaction times*

We monitored decision confidence and reaction-times (in an un-speeded task) while participants made numerosity judgements after adaptation, either to dense visual patterns or to hand-tapping. The major results were obtained from analysis of the “aggregate observer”, pooling data over all 12 participants (10 in the adaptation to hand-tapping). However, we also analysed individual data from all participants separately and, although the reduced data were necessarily more noisy, the group analysis gave essentially the same results as the aggregate. The results of the individual analyses are reported in the supplementary material, and summarised in Figure S4 and table S1.

Figure 3 shows the main results from the aggregate data. Figures 3A&B are psychometric functions, plotting the proportion of trials (for all participants) where the test was reported as more numerous than the reference, as a function of the numerosity of the test patch. Both data sets were well fit by cumulative Gaussian error functions, which were clearly displaced by adaptation, both by visual dot-patterns and hand-tapping. In the un-adapted condition (Figure 3A, blue symbols and curves), the psychometric function was centred at 17 dots, very near the actual reference of 16 dots. Visual adaptation to 60 dots clearly displaced the psychometric function rightwards, shifting the median (which estimates the PSE) to 22.7 dots, meaning that after adaptation the probe needed to be 33% more numerous than the reference to appear equal to it. A similar effect occurred for hand-tapping: slow tapping had little effect, with the PSE remaining at 15.9 (near the reference), while fast tapping increased it to 18.1, again implying a decrease of apparent numerosity, in this case of 14%.

Both the confidence and mean reaction-time data were well fit by Gaussian functions ( $R^2 > 0.75$  in all cases). The peaks of these functions (indicated by the arrows, and reported in table S1), clearly also shift with adaptation, both to visual numerosity and hand-tapping. The shift is in the same direction as the shift in PSEs, tending to align peaks in confidence and reaction-times with the PSEs. These results on the aggregate observer are very similar to those obtained from analysis of individual participants (see supplemental material)

The blue and red histograms of Figure 4 (A-D) show the results of bootstrapping (10,000 repetitions, sampling with replacement). On each repetition, estimates were made for PSE, point of *minimal confidence* and *maximal reaction-time*. It is clear from inspection that in all cases the distributions for the investigated conditions overlap very little, indicating that they are significantly different. Bootstrap sign test yielded significance levels of  $p < 0.003$  in all cases. On adaptation to visual stimuli peaks in both the confidence (Figure 4 A) and reaction-time (Figure 4 C) were higher for the adapt-high condition than baseline in all 10,000 iterations ( $p < 10^{-4}$ ). On adaptation to tapping, peaks in confidence (Figure 4 B) were lower for the adapt-high than adapt-low condition on only 34 iteration ( $p = 0.0034$ ), and for reaction-times (Figure 4 D) only 20 times ( $p = 0.002$ ) out of 10,000.

We then used the bootstrapped distributions to pit two plausible models against each other: 1) that the shifts in the psychometric functions result from a response strategy for uncertain trials [13: illustrated in Figure 1]; 2) that the change reflects adaptation-induced changes within sensory circuits. Model 1 predicts that the confidence and reaction-time distributions should not move with adaptation, so those for the adapt-high should be closer to  $PSE_{base}$  (or  $PSE_{low}$ ) than to  $PSE_{high}$ . On the other hand, model 2 predicts that both peaks should follow the shifts in PSE, and therefore be closer to  $PSE_{high}$ . We tested this by bootstrap sign test, counting how many iterations

were closer to  $PSE_{base}$  (or  $PSE_{low}$ ) than  $PSE_{high}$ . We also bootstrapped the PSEs themselves on each iteration, to include their error in the calculation (the orange distribution in Figure 4 shows the bootstrapped mid-points of the two PSEs). For visual adaptation, not a single iteration of either confidence or reaction-time peaks was closer to  $PSE_{base}$  than  $PSE_{high}$ , implying the likelihood for the first model is  $p < 10^{-4}$ . The tapping condition also showed a clear effect. For the confidence data, the likelihood of model 1 was  $p = 0.05$ , compared with  $p = 0.95$  for model 2, giving a likelihood ratio of 19. Reaction-times were more significant, with likelihood of model 1 equal to 0.0064 compared with 0.9936 for model 2, 166 times less likely. All the bootstrapped sign tests provide strong evidence for model 2 for both types of adaptation, suggesting that the adaptation occurs within sensory rather than decision systems.

234

235 ----- FIGURE 4 -----

236

To test the validity of the confidence ratings, we separated the data into high- and low-confidence trials and fitted psychometric functions separately for each, calculating the just noticeable difference (JND), from the standard deviation of the fit. Standard errors and significance were calculated by bootstrap. As there were 3 times as many trials judged confident than unconfident, the data for confident judgements were under-sampled during bootstrapping to match sample sizes. Figures 5A&B show JNDs for the high-confidence trials were significantly lower than that for low-confidence, by at least a factor of two ( $p < 10^{-4}$  in all cases), consistent with the idea that subjective confidence reflects a genuine metacognitive ability which assesses the quality of sensory evidence [16].

We also correlated reaction-times against confidence (Figures 5C&D). Each point of Figure 5C comes from Figures 3C&E, and those from Figure 5D from Figures 3D&F. The correlation was strong, with  $r = -0.87$  and  $-0.89$  for the two

adaptation types, accounting for more than 70% of the variance. This shows that the two measures covary together, consistent with their being driven by a common factor, most probably perceived stimulus strength.

253

254 ----- FIGURE 5 -----

255

256 *Control experiment: Effects of reward on confidence and reaction times*

257 In order to show that confidence and reaction times do not necessarily change with  
258 PSE, we devised a control experiment where we manipulated rewards. Here there was  
259 no adaptation, but participants played a point-based game, with three types of reward  
260 regimes (in different blocks). In baseline blocks, they received 1 point for each correct  
261 response and lost 1 for every error (performing on average at 85% correct). In “reward-  
262 low” blocks, they received 2 points for correctly responding “less than”, and lost 1 each  
263 error; and in “reward-high”, 2 points for correctly responding “greater than”, losing 1  
264 for an error. This simple reward manipulation of rewards biased observers towards the  
265 double-reward response when uncertain, causing robust shifts in the PSE. Figure 6 A  
266 shows the psychometric functions for the aggregate observer for the three conditions.  
267 The PSE for the standard condition was 17.5 (a constant bias of 1.5 from the physical  
268 equivalent of 16), while for the “reward-low” condition it was 15.8 (1.7 lower) and for  
269 “reward-high” was 19.1 (1.6 higher). Both cases are near the predictions of the ideal  
270 observer (which predicts a shift of 1.2 towards the rewarded side).

271 However, the shift in PSE was not accompanied by concomitant shifts in  
272 confidence: the minima in the gaussians are very similar for all three conditions (17.4,  
273 17.1 & 18.0 for low, baseline and high). Similarly, the peak reaction times did not  
274 follow the PSEs, but again tended to cluster around the baseline PSE (16.3, 17.3 &  
275 17.6). The histograms below the confidence and RT curves show the bootstrap  
276 analysis, similar to that of Figure 4. The bootstraps clearly overlap considerably.  
277 Again, we tested the two plausible models outlined for Figure 4, counting, for each

condition, how many iterations were nearer to the PSE of that condition rather than to the PSE of the baseline (non-rewarded) condition. For the confidence measures the results were clear: the probabilities of model 2 (closer to the shifted PSE) being correct were  $p=0.046$  for the reward-low condition, and  $p=10^{-4}$  for the reward-high condition, 20 and 10,000 times less likely than model 1. The results for reaction times was similarly in favour of model 1, with probabilities for model 2 at  $p<10^{-4}$  for the reward-low condition, and  $p=0.012$  for the reward-high condition, infinite and 81 times less likely than model 1. Reaction times in this experiment may have been less reliable, because of variable slowing when integrating the reward “*prior*”. Again, the results from the aggregate observer are very similar to those obtained from analysis of individual participants (see supplemental material).

289

290 ----- FIGURE 6 -----

291

## 292 **Discussion**

293 The primary goal of this study was to probe the mechanisms of numerosity adaptation, 294 to test whether adaptation affects sensory processing mechanisms directly, or indirectly 295 via decision or response criteria. We argue that a change in sensory processing should 296 result in a comparable change in minimum decision confidence and maximum 297 reaction-times, which should shift to align with the point of subjective equality after 298 adaptation, where the test and probe stimuli are, by definition, most similar 299 perceptually. On the other hand, if the change in PSE results from a response bias, the 300 peaks in confidence and reaction-times should not change with adaption (see Figure 301 1). Our results clearly support the claim that adaptation affects sensory processing 302 directly. Two types of adaptation – to visual patterns and to hand-tapping – caused 303 large shifts in PSEs, with concomitant shifts in peak confidence and reaction-times. In 304 all cases, the sensory processing model was far more probable than that suggested by 305 confidence-induced shifts in response criteria. On the other hand, when the PSEs were

306 shifted by awarding rewards for specific responses, the shifts in PSE were not  
307 accompanied by shifts in confidence or RTs.

308         The results are interesting for several reasons. Firstly, there has been a long-  
309 standing debate about the nature of numerosity processing, particularly about whether  
310 it is sensed directly, or is a by-product of texture processing [17,18]. One of the  
311 strongest lines of evidence that numerosity is distinct from texture density comes from  
312 adaptation studies, particularly cross-modal and cross-format adaptation [7]: adapting  
313 to sequences of flashes or tones affects the perceived numerosity of dot arrays, difficult  
314 to ascribe to texture perception. The demonstration that adaptation to fast or slow hand-  
315 tapping changes the perceived numerosity of spatial arrays is even more fascinating,  
316 as it links perception and action, implicating common mechanisms for perceiving and  
317 reproducing numerosity [8].

318         However, paraphrasing Laplace [19]: “extraordinary claims require  
319 extraordinary evidence”. It is therefore reasonable to expect a rigorous demonstration  
320 that motor tapping affects the perception of numerosity directly, rather than merely  
321 biasing the decision or the response along the lines of Figure 1. The fact that all  
322 analyses show that both confidence and reaction-time peaks move to the adapted PSE  
323 strongly favours the hypothesis that adaptation causes changes at the sensory level.  
324 This has important ramifications for understanding the role of numerosity mechanisms  
325 in perception and action, relating well to the electrophysiological studies showing a  
326 clear selectivity for the number of self-produced actions in the area 5 of the superior  
327 parietal lobule of monkey [10,20].

328         The other more general result of this study is a method of validating adaptation  
329 and other effects of temporal and spatial dependency (such as serial dependence [21–  
330 24]. Adaptation is a fundamental tool in psychophysics, famously referred to as “the  
331 psychophysicist’s microelectrode” [11]. However, adaptation studies necessarily rely  
332 on subjective judgements, on participants reporting their subjective impressions. Most  
333 modern adaptation studies use two-alternative forced choice techniques that ask  
334 participants to compare the adapted test to a probe, yielding psychometric functions

335 from which the point of subjective equality can be titrated. However, unlike other  
336 forced choice tasks (such as measurement of contrast sensitivity), there is no right or  
337 wrong answer: just a subjective judgment that stimulus A was larger, brighter or more  
338 numerous than stimulus B. Over a considerable range around the point of subjective  
339 equality, judgments are difficult, but participants must respond, guessing if unsure. It  
340 requires only a slight tendency to respond stereotypically in one direction when unsure  
341 to shift the curves, robustly changing the PSE, without changing the slope of the  
342 function [13]. It therefore becomes important to have objective corroborative evidence  
343 that the point of subjective equality really reflects sensory changes rather than response  
344 biases. Gallagher et al. [14] suggested that minima in response criteria could provide  
345 useful corroboration, and demonstrated that it can do so for motion adaption (and also  
346 for serial dependence). We extend their idea, showing that even with a far more subtle  
347 forms of adaptation elicited by hand-tapping, the minima in confidence follow the  
348 changes in PSE.

349         We point out that we are testing a specific model of how decision criteria may  
350 affect PSEs: that a small tendency of response bias could affect trials of low  
351 confidence, causing reliable shifts in PSE [13]. With this particular model, as  
352 confidence is driving the response, it is unlikely to shift with the response PSE.  
353 However, other more complex models of perceptual decisions [25,26] may predict that  
354 confidence and RT do change with changes in PSE. Indeed, with these classes of  
355 models it is often difficult to distinguish experimentally between sensory and  
356 perceptual decision effects [27]. We therefore designed a realistic experiment that  
357 manipulated PSEs at the decisional level, by rewarding correct responses in a specific  
358 direction (high or low). This produced robust changes in responses, shifting the PSE  
359 as expected, as participants sought to optimize gains: however, the shifts in PSE were  
360 not accompanied by concomitant changes in confidence, nor in RTs. This is a clear  
361 existence proof that at least some types of manipulation on decisions are not paralleled  
362 by shifts in confidence, which may therefore be a signature of sensory changes.  
363 Gallagher et al. [14] performed a similar experiment, instructing participants



specifically to respond “left” or “right” when confidence is low, and also showed that this manipulation does not shift the point of minimal confidence. However, our task was more natural, in that we gave no instructions to participants on how to respond, nor that they should take confidence into account. It was a natural task with greater risks on one side than the other (like those pioneered by Trommershäuser and colleagues [28]) which human participants soon learn to optimize. Yet this very natural and spontaneous task, which shifted PSEs smoothly, caused no similar shifts in confidence or RTs.

In general, reaction-times provided more robust data than confidence for the sensory shifts in PSE. Reaction times could have several advantages to confidence measures. Firstly, they are objective and come at no extra cost, automatically encoded in the timestamps of the stimuli and responses, without having to ask participants to make a second response. Nor was it necessary to ask for a speeded response; we simply relied on the tendency of participants to respond reasonably quickly in order to finish the session as soon as possible. For the adaptation experiments, reaction-times proved to be more informative than confidence, in all cases providing stronger evidence for a shift in their peak. For example, for the aggregate data for adaptation to tapping, the  $\text{Log}_{10}\text{BF}_{12}$  was 1.26 for confidence, compared with 2.22 for reaction-time data. For the analysis of individual data (where there are far fewer trials, hence more noisy estimates) the  $\text{Log}_{10}\text{BF}_{12}$  for confidence was 1.14 compared with 2.46 for reaction-times. In all cases the  $\log_{10}$ -Bayes factors were greater than 1, considered *strong* evidence, but the reaction-time data gave  $\log_{10}\text{BF} > 2$ , considered *decisive* [29]. There is considerable evidence showing that reaction times vary monotonically with signal strength [15], and should therefore be maximal at the point of least difference in the signals. Combined with the ease with which reaction-time data can be collected, with no additional load on participants, it would appear to be the preferred method.

To summarize, we present a new technique for investigating the mechanisms of numerosity adaptation and sensory adaptation in general. By simultaneously measuring subjective confidence and more importantly – reaction-times, we demonstrate that

393 adaptation to numerosity, either by observing visual stimuli of high numerosity or by  
394 subjects tapping in a particular region occurs at a sensory level, before stages of  
395 perceptual decision. Adaptation affects not only perceived numerosity, but also  
396 subjective confidence and reaction-times, showing that they are a consequence of  
397 sensory adaptation, rather than the cause for the shift in the psychometric functions.

398

399

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401

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#### 409 **Data accessibility**

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411 The data that support the findings of this study are available online at: Dryad doi:  
412 10.5061/dryad.95x69p8gh

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## References

1. Mollon JD. 1974 After-effects and the brain. *New Sci.* **61**, 479–482.
2. Leopold DA, Rhodes G, Müller KM, Jeffery L. 2005 The dynamics of visual adaptation to faces. *Proc. R. Soc. B Biol. Sci.* **272**, 897–904. (doi:10.1098/rspb.2004.3022)
3. Thompson P, Burr D. 2009 Visual aftereffects. *Curr. Biol.* **19**, R11–14. (doi:10.1016/j.cub.2008.10.014)
4. Burr D, Ross J. 2008 A Visual Sense of Number. *Curr. Biol.* **18**, 425–428. (doi:10.1016/j.cub.2008.02.052)
5. Butterworth B. 2008 Numerosity Perception: How Many Speckles on the Hen? *Curr. Biol.* **18**, R388–R389. (doi:10.1016/j.cub.2008.03.014)
6. Castaldi E, Aagten-Murphy D, Tosetti M, Burr D, Morrone MC. 2016 Effects of adaptation on numerosity decoding in the human brain. *Neuroimage* **143**, 364–377. (doi:10.1016/j.neuroimage.2016.09.020)
7. Arrighi R, Togoli I, Burr DC. 2014 A generalized sense of number. *Proc. R. Soc. B Biol. Sci.* **281**. (doi:10.1098/rspb.2014.1791)
8. Anobile G, Arrighi R, Togoli I, Burr DC. 2016 A shared numerical representation for action and perception. *Elife* **5**. (doi:10.7554/eLife.16161)
9. Nieder A, Dehaene S. 2009 Representation of Number in the Brain. *Annu. Rev. Neurosci.* **32**, 185–208. (doi:10.1146/annurev.neuro.051508.135550)
10. Sawamura H, Shima K, Tanji J. 2002 Numerical representation for action in the parietal cortex of the monkey. *Nature* **415**, 918–922. (doi:10.1038/415918a)
11. Frisby JP. 1979 *Seeing: Illusion, Brain and Mind*. Oxford: Oxford University Press.
12. Firestone C, Scholl BJ. 2016 Cognition does not affect perception: Evaluating the evidence for “top-down” effects. *Behav. Brain Sci.* **39**, e229.

- (doi:10.1017/S0140525X15000965)
13. Morgan M, Dillenburger B, Raphael S, Solomon JA. 2011 Observers can voluntarily shift their psychometric functions without losing sensitivity. *Attention, Perception, Psychophys.* **74**, 185–193. (doi:10.3758/s13414-011-0222-7)
  14. Gallagher RM, Suddendorf T, Arnold DH. 2019 Confidence as a diagnostic tool for perceptual aftereffects. *Sci. Rep.* **9**. (doi:10.1038/s41598-019-43170-1)
  15. Piéron H. 1914 II. Recherches sur les lois de variation des temps de latence sensorielle en fonction des intensités excitatrices. *Annee. Psychol.* **20**, 17–96. (doi:10.3406/psy.1913.4294)
  16. Mamassian P. 2016 Visual Confidence. *Annu. Rev. Vis. Sci.* **2**, 459–481. (doi:10.1146/annurev-vision-111815-114630)
  17. Anobile G, Cicchini GM, Burr DC. 2016 Number As a Primary Perceptual Attribute: A Review. *Perception* **45**, 5–31. (doi:10.1177/0301006615602599)
  18. Burr DC, Anobile G, Arrighi R. 2018 Psychophysical evidence for the number sense. *Philos. Trans. R. Soc. B Biol. Sci.* **373**. (doi:10.1098/rstb.2017.0045)
  19. Laplace PS. 1812 Théorie analytique des Probabilités. In 2, Paris: Courcier Imprimeur.
  20. Sawamura H, Shima K, Tanji J. 2010 Deficits in action selection based on numerical information after inactivation of the posterior parietal cortex in monkeys. *J. Neurophysiol.* **104**, 902–910. (doi:10.1152/jn.01014.2009)
  21. Cicchini GM, Anobile G, Burr DC. 2014 Compressive mapping of number to space reflects dynamic encoding mechanisms, not static logarithmic transform. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 7867–7872. (doi:10.1073/pnas.1402785111)
  22. Cicchini GM, Mikellidou K, Burr D. 2017 Serial dependencies act directly on perception. *J. Vis.* **17**, 6. (doi:10.1167/17.14.6)
  23. Fischer J, Whitney D. 2014 Serial dependence in visual perception. *Nat.*

- 505       *Neurosci.* **17**, 738–743. (doi:10.1038/nn.3689)
- 506   24.   Fornaciai M, Park J. 2019 Serial dependence generalizes across different  
507       stimulus formats, but not different sensory modalities. *Vision Res.* **160**, 108–  
508       115. (doi:10.1016/j.visres.2019.04.011)
- 509   25.   Ratcliff R, McKoon G. 2008 The diffusion decision model: Theory and data for  
510       two-choice decision tasks. *Neural Comput.* **20**, 873–922.  
511       (doi:10.1162/neco.2008.12-06-420)
- 512   26.   Maniscalco B, Lau H. 2014 Signal detection theory analysis of type 1 and type  
513       2 data: Meta- $d'$ , response-specific meta- $d'$ , and the unequal variance SDT  
514       model. In *The Cognitive Neuroscience of Metacognition*, pp. 25–66. Springer  
515       Berlin Heidelberg. (doi:10.1007/978-3-642-45190-4\_3)
- 516   27.   Pelli DG. 1985 Uncertainty explains many aspects of visual contrast detection  
517       and discrimination. *J. Opt. Soc. Am. A* **2**, 1508–1532.  
518       (doi:10.1364/josaa.2.001508)
- 519   28.   Trommershäuser J, Gepshtein S, Maloney LT, Landy MS, Banks MS. 2005  
520       Optimal compensation for changes in task-relevant movement variability. *J.*  
521       *Neurosci.* (doi:10.1523/JNEUROSCI.1906-05.2005)
- 522   29.   Jeffreys H. 1998 *Theory of probability*. 3rd edn. Oxford: Clarendon Press.

## 531 Captions

532 **Figure 1.** Simulation showing how response biases could induce a shift in psychometric function resembling a real  
533 sensory change. The red curve shows a hypothetical psychometric function for a numerosity discrimination task. The blue  
534 curve plots confidence level based on the relative numerosity difference between the stimuli. The green curve shows the  
535 result of a decision strategy “less if unconfident”, obtained by the pointwise product of two functions.

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538 **Figure 2.** Stimuli and procedure. On each trial subjects were required to which of two stimuli were more numerous, then  
539 indicate whether they were confident with their response (both responses 2AFC). In the visual adaptation condition, a  
540 dense dot array was displayed first for 40 s than for 6 s top-up periods at the test location before the discrimination task  
541 (top left). In the motor adaptation condition (top right), participants were required to tap their hand with index finger  
542 extended, for 6 s on the right side of the screen, with their hand concealed by the screen and without touching any surface  
543 to minimize sensory feedback. Subjects either tapped as fast as possible or slowly, at around 1 Hz (tested in separated  
544 sessions). In all conditions, reaction times between the offset of the reference and the numerosity response were measured,  
545 although participants were never requested to make any speeded response.

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548 **Figure 3.** A-B: Psychophysical functions showing proportion of trials in which the test was perceived more numerous  
549 than the reference, as a function of test numerosity. C-D: Confidence levels and mean reaction times (E-F) as a function  
550 of test numerosity, for visual and motor adaptation (left and right panels respectively). In all graphs, blue and red curves  
551 indicate baseline and high adaptation for visual adaptation (panels on left hand side) and slow or fast tapping in the motor  
552 experiment (on right hand side). The dashed lines show the PSEs and arrows the peaks of the best-fit gaussians to the  
553 confidence or reaction time distributions.

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556 **Figure 4.** Frequency distributions of bootstraps for confidence (A-B) and reaction-times (C-D), for visual or motor  
557 adaptation experiment (left and right panels respectively). Data in blue represent visual baseline or slow tapping condition  
558 and red for high visual adaptation or fast motor tapping). Orange distributions show the bootstrapped mid-points between  
559 baseline (or slow) and adaptation (or fast tapping) PSEs.

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562 **Figure 5.** Bar graphs show precision for numerosity discrimination in the high or low confidence trials. In blue, data for  
563 baseline (or slow tapping) and red data for adaptation to high (or fast tapping) for visual and motor adaptation. (C-D)  
564 Reaction-times (averaged over trials and subjects) as a function of confidence (averaged over trials and subjects) for the  
565 two adaptation conditions. Black lines represent the best-fitting linear regressions (C visual adaptation:  $R^2 = 0.76$ ; D  
566 motor adaptation:  $R^2 = 0.79$ ). Error bar represent  $\pm 1$  s.e.m., \*\*\*  $p < 0.0001$ .

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569 **Figure 6.** (A) Psychophysical functions of proportion of trials when the test was seen as more numerous than the neutral  
570 probe, as a function of physical numerosity in the control condition (baseline in orange, leftward condition in blue and  
571 rightward condition in red). (C) Expressions of confidence, as a function of physical numerosity. (C) Mean reaction-times  
572 (in seconds) as a function of physical numerosity. The continuous dotted lines indicate the PSE of the psychophysical  
573 curves. The histograms below the confidence and reaction time fits represent the bootstrap analysis.

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