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

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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 ± 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;

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

167

168

169 Results*170 Effects of adaptation on confidence and reaction times*

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

180 Figure 3 shows the main results from the aggregate data. Figures 3A&B are
181 psychometric functions, plotting the proportion of trials (for all participants) where the
182 test was reported as more numerous than the reference, as a function of the numerosity
183 of the test patch. Both data sets were well fit by cumulative Gaussian error functions,
184 which were clearly displaced by adaptation, both by visual dot-patterns and hand-
185 tapping. In the un-adapted condition (Figure 3A, blue symbols and curves), the
186 psychometric function was centred at 17 dots, very near the actual reference of 16 dots.
187 Visual adaptation to 60 dots clearly displaced the psychometric function rightwards,
188 shifting the median (which estimates the PSE) to 22.7 dots, meaning that after
189 adaptation the probe needed to be 33% more numerous than the reference to appear
190 equal to it. A similar effect occurred for hand-tapping: slow tapping had little effect,
191 with the PSE remaining at 15.9 (near the reference), while fast tapping increased it to
192 18.1, again implying a decrease of apparent numerosity, in this case of 14%.

193

194

----- FIGURE 3 -----

195

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

203 The blue and red histograms of Figure 4 (A-D) show the results of bootstrapping
204 (10,000 repetitions, sampling with replacement). On each repetition, estimates were
205 made for PSE, point of *minimal confidence* and *maximal reaction-time*. It is clear from
206 inspection that in all cases the distributions for the investigated conditions overlap very
207 little, indicating that they are significantly different. Bootstrap sign test yielded
208 significance levels of $p < 0.003$ in all cases. On adaptation to visual stimuli peaks in
209 both the confidence (Figure 4 A) and reaction-time (Figure 4 C) were higher for the
210 adapt-high condition than baseline in all 10,000 iterations ($p < 10^{-4}$). On adaptation to
211 tapping, peaks in confidence (Figure 4 B) were lower for the adapt-high than adapt-
212 low condition on only 34 iteration ($p = 0.0034$), and for reaction-times (Figure 4 D)
213 only 20 times ($p = 0.002$) out of 10,000.

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

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

234

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

236

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

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

250 adaptation types, accounting for more than 70% of the variance. This shows that the
251 two measures covary together, consistent with their being driven by a common factor,
252 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

278 condition, how many iterations were nearer to the PSE of that condition rather than to
279 the PSE of the baseline (non-rewarded) condition. For the confidence measures the
280 results were clear: the probabilities of model 2 (closer to the shifted PSE) being correct
281 were $p=0.046$ for the reward-low condition, and $p=10^{-4}$ for the reward-high condition,
282 20 and 10,000 times less likely than model 1. The results for reaction times was
283 similarly in favour of model 1, with probabilities for model 2 at $p<10^{-4}$ for the reward-
284 low condition, and $p=0.012$ for the reward-high condition, infinite and 81 times less
285 likely than model 1. Reaction times in this experiment may have been less reliable,
286 because of variable slowing when integrating the reward “*prior*”. Again, the results
287 from the aggregate observer are very similar to those obtained from analysis of
288 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

364 specifically to respond “left” or “right” when confidence is low, and also showed that
365 this manipulation does not shift the point of minimal confidence. However, our task
366 was more natural, in that we gave no instructions to participants on how to respond,
367 nor that they should take confidence into account. It was a natural task with greater
368 risks on one side than the other (like those pioneered by Trommershäuser and colleagues
369 [28]) which human participants soon learn to optimize. Yet this very natural and
370 spontaneous task, which shifted PSEs smoothly, caused no similar shifts in confidence
371 or RTs.

372 In general, reaction-times provided more robust data than confidence for the
373 sensory shifts in PSE. Reaction times could have several advantages to confidence
374 measures. Firstly, they are objective and come at no extra cost, automatically encoded
375 in the timestamps of the stimuli and responses, without having to ask participants to
376 make a second response. Nor was it necessary to ask for a speeded response; we simply
377 relied on the tendency of participants to respond reasonably quickly in order to finish
378 the session as soon as possible. For the adaptation experiments, reaction-times proved
379 to be more informative than confidence, in all cases providing stronger evidence for a
380 shift in their peak. For example, for the aggregate data for adaptation to tapping, the
381 $\text{Log}_{10}\text{BF}_{12}$ was 1.26 for confidence, compared with 2.22 for reaction-time data. For the
382 analysis of individual data (where there are far fewer trials, hence more noisy
383 estimates) the $\text{Log}_{10}\text{BF}_{12}$ for confidence was 1.14 compared with 2.46 for reaction-
384 times. In all cases the \log_{10} -Bayes factors were greater than 1, considered *strong*
385 evidence, but the reaction-time data gave $\log_{10}\text{BF} > 2$, considered *decisive* [29]. There
386 is considerable evidence showing that reaction times vary monotonically with signal
387 strength [15], and should therefore be maximal at the point of least difference in the
388 signals. Combined with the ease with which reaction-time data can be collected, with
389 no additional load on participants, it would appear to be the preferred method.

390 To summarize, we present a new technique for investigating the mechanisms of
391 numerosity adaptation and sensory adaptation in general. By simultaneously measuring
392 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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407 serial dependence and rhythmic oscillations’).

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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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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 ± 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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