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HOW FAST DO MOBILE ORGANISMS RESPOND TO STIMULI?

RESPONSE TIMES FROM BACTERIA TO ELEPHANTS AND WHALES

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22 SUMMARY

23

24 Quick responses to fast changes in the environment are crucial in animal behaviour and survival,

25 for example to seize prey, escape predators, or negotiate obstacles. Here, we study the 'simple

26 response time' that is the time elapsed between receptor stimulation and motor activation as

27 typically shown in escape responses, for mobile organisms of various taxa ranging from bacteria

28 to large vertebrates. We show that 95 % of these simple response times lie within one order of

29 magnitude of the overall geometric mean of about 25 ms, which is similar to that of a well-

30 studied sensory time scale, the inverse of the critical flicker fusion frequency in vision, also lying

31 within close bounds for all the organisms studied. We find that this time scale is a few times

32 smaller than the minimum time to move by one body length, which is known to lie also within a

33 relatively narrow range for all moving organisms. The remarkably small 10^2-fold range of the

34 simple response time among so disparate life forms varying over 10^{20}-fold in body mass suggests

35 that it is determined by basic physicochemical constraints, independently on the structure and

36 scale of the organism. We thus propose first-principle estimates of the simple response and

37 sensory time scales in terms of physical constants and a few basic biological properties common

38 to mobile organisms and constraining their responses.

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1. INTRODUCTION

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42   The concept of timescale is fundamental in science. An important timescale in biology is the

43   minimum response time of mobile organisms to a dynamic environment. When an animal

44   suddenly encounters a prominent event such as a prey, a predator or an obstacle, it must react

45   fast enough, albeit not faster than necessary, in order not to sacrifice accuracy or waste the

46   energy or space dedicated to its sensory systems (e.g. Attwell and Laughlin 2001). For a

47   response to be fast enough, the information that produced the response should not be outdated

48   (e.g. Spence 2009), which requires in particular that the response time does not exceed the

49   movement duration and that the animal position has not changed much. For animals moving with

50   legs, the response time is often compared to the stance or step duration (e.g. More et al. 2018);

51   however, for animals not equipped with legs, a more general time scale for comparison with the

52   minimum response time is the minimum time to move by one body length, that is the ratio of

53   body length to maximum speed.

54   The maximum speed of terrestrial and aquatic organisms has been found to be roughly

55   proportional to their body length, from bacteria to large vertebrates (Bonner 1965, McMahon and

56   Bonner 1983), contrary to the preferred speed which is subjected to different constraints (e.g.

57   Bejan and Marden 2006). These results, later confirmed with a large data set, imply that the time

58   to move by one body length at maximum speed lies in a narrow range around one tenth of

59   second within a factor of ten, for running and swimming organisms of mass varying by 10^{20}-fold

60   in body mass. The ubiquity of this minimum locomotion time scale, holding for so different

61   organisms' structures and sizes, whereas characteristic biological timescales cover more than 12

62   orders of magnitude (e. g. Shamir et al. 2016), suggests that it is bounded by universal

63   constraints, and led Meyer-Vernet and Rospars (2015, 2016) to propose a tentative interpretation

64　based on the mass density of living organisms, the maximum specific tension exerted by

65　molecular motors and muscles (Rospars and Meyer-Vernet 2016) and the maximum mass

66　specific metabolic rate (Weibel and Hoppeler 2005, Glazier 2014, Makarieva et al. 2005), which

67　constrain the maximum speed and remain within close bounds for all moving organisms.

68　　　The question therefore arises of whether a similar result could hold for the minimum time to

69　react to stimuli. The scaling of sensorimotor delays with body mass in relation to movement

70　duration has been studied by More and Donelan (2018) for the stretch reflex in terrestrial

71　mammals, but there is no large-scale study of the minimum response time covering the entire

72　mass range of mobile species. We therefore collated data from the literature for the 'simple

73　response time', that is the time to detect the occurrence of a simple stimulus, as determined from

74　behavioural and electrophysiological measurements in various taxa from free-living cells to large

75　metazoans like sharks, turtles, and elephants, spanning 20 orders of magnitude in mass from

76　10^{-16} to 3900 kg.

77　　　An important constraint to fast response is set by sensory limitations that affect the ability to

78　track fast moving objects such as prey or mates. These limitations have been studied in the case

79　of vision, using the critical flicker fusion frequency (CFF), defined as the frequency at which a

80　flickering light is indistinguishable from a continuous light (e.g. D'Eath 1998). The scaling of

81　this property with body mass and metabolism has been studied by Healy et al. (2013) for

82　vertebrates; we collated the corresponding characteristic time (1/CFF) and extended the data to

83　compare it to the minimum response time.

84　　　Our aims are (i) to determine whether the minimum response time remains within close

85　bounds across the whole of mobile life despite the diversity of structures and mechanisms, (ii) to

86　compare it with the minimum sensory time-scale for vision (inverse of the critical flicker fusion

87　frequency) and to the minimum time to move by one body length, and (iii) to propose an

88 interpretation based on basic physicochemical and biological properties. Because the response

89 times of animals are expected to be hugely different from those of microorganisms, which are

90 subjected to very different constraints (e.g. Martens et al. 2015), we also investigate the

91 timescales separately for single cells and for metazoans.

92   The empirical data are studied and discussed in sections 2 to 4. Section 5 proposes order-of-

93 magnitude interpretations based on fundamental physicochemical constants and basic properties

94 of life, with conclusions given in Section 6.

95

96 2. MATERIAL AND METHODS

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98 2.1. *Data Collection*

99

100 We define as "simple response time" (T_S) the time to detect the occurrence of a simple and

101 sudden stimulus. These T_S are delays from the time at which the stimulus reaches the organism to

102 either the onset of movement – measured by behavioural methods (for example with high-speed

103 cinematography), or to muscle activation – measured by electrophysiological methods with direct

104 recordings from muscles (electromyogram EMG). Since our study concerns minimum response

105 times, it does not include the "discrimination (or identification) and choice response times" (e.g.

106 Luce 1991). In these complex tasks, the subject, whether animal or human, is presented with one

107 of several stimuli and has to respond to only one of them (discrimination, e.g. Blough 1978) or to

108 perform different responses depending on the stimulus presented (choice between stimuli, e.g.

109 Abraham et al. 2004). Likewise, for microorganisms, we only considered the response delay after

110 a stimulus (e.g. Block et al. 1982), which only involves internal time scales of the organisms and

111 is shorter than the time based on the comparison of different measurements, which depends on

112   ambient conditions (e.g. Mitchell 1991). Thus, our definition of simple response times T_S being

113   based on the simplicity of the task and the stimulus does not take into account the length,

114   variability or underlying sensorimotor mechanisms of the response delays (Roeder 1963, Koch

115   1999, Herberholz and Marquart 2012, Sillar et al. 2016, Roberts et al. 2019). It avoids the

116   operational difficulty to implement these multiple criteria and insures a better representativeness

117   of the sample.

118   We searched the Google Scholar database and extracted simple response times and other

119   relevant data (species names, stimuli, experimental conditions, etc.) published in refereed

120   journals. Our main objective being to investigate the interspecific variability, we kept all values

121   found for non-human species, but not for humans, for which we considered only a selection of

122   papers, either classical or illustrating the diversity of experimental paradigms. For a given species

123   and stimulus, we tabulated simple response times as the mean provided by the authors, or the

124   mean of the extremes when given as a range.

125   Our T_S sample (Table S1) includes 175 measurements on 81 species. Behavioural ($n = 134$)

126   and electromyographic (EMG, $n = 41$) measurements (column M in Table S1) are not

127   significantly different (Fig. S2A and Table S10); thus, we pooled them together in subsequent

128   analyses. The data belong to two main classes: startle and non-startle. "A startle response is an

129   abrupt response, often of relatively short latency, to a sudden stimulus that we believe to be both

130   unexpected and alarming (i.e., of high valence)" (Bullock 1984), so that threats that develop

131   gradually are excluded. Startle responses form a homogeneous class gathering the majority of

132   measurements (73 %) and of species (68 %, multicellular only). They may result in a large

133   movement translating the whole body (escape, called fast-start in fishes, 86 measurements on 50

134   species) or in small movements (called sometimes 'eyelid, jaw, etc. reflex' in birds and

135   mammals, depending on the muscle triggered, 42 measurements in five species). Non-startle

136   responses (27 % of measurements on 32 % of species) include taxes (in single cells only), reflex

137   control of locomotion, fast limb movements, predatory movements, and a few other fast

138   responses in multicellular organisms. Only six species were tested for more than one response

139   type.

140   For flicker fusion times T_F, we used the CFF data from Healy et al. (2013) (34 vertebrate

141   species) and Inger et al. (2014) (31 invertebrate species and 41 vertebrate species not considered

142   by Healy et al. 2013), plus 25 other CFF measurements. Our sample (T_F = 1/CFF, Table S2)

143   includes 130 measurements on 108 species. The values measured by behavioural ($n = 26$) and

144   electroretinographic (ERG, $n = 103$, column M in Table S2) techniques are not significantly

145   different (Fig. S2C and Table S10); so, we pooled them together.

146   The minimum times to move by one body length T_L were collected and analysed previously

147   from the measured maximum speeds V_{max} of swimming and running organisms of length L as T_L

148    $= L/V_{max}$; this sample includes 458 measurements from 427 species (Table S3) and does not

149   include flying, whose maximum speed is not constrained by muscles (Meyer-Vernet and Rospars

150   2016).

151   For T_S and T_L, we distinguished unicellular and multicellular organisms and spermatozoids (T_L

152   only), as specified in column U of Tables S1 and S3. For the three timescales, column Cla of

153   Tables S1-S3 defines groups of phylogenetically related species; they belong to the same class in

154   multicellular organisms and to the same kingdom according to the WoRMS database (World

155   Register of Marine Species, http://www.marinespecies.org) in unicellular organisms (except

156   spermatozoids). Further details on Tables S1-S3 are given in Supplementary material.

157   Table S4 lists 14 mammalian species for which both minimum locomotor times T_L and

158   maximum mass specific metabolic rates (MSMR in W/kg) are known.

159

160 2.2. *Body Mass*

161

162 We characterized body size by the mass *M* for each species. Except for vertebrates with measured

163 CFFs from Healy et al. (2013) for which we used the mass provided by these authors, we

164 searched the original papers for mass, length or age. When given as a range, we took the mean.

165 We converted length in mass using either the length-mass relationship of the species when it is

166 known or a more generic relationship, for example $M_{kg} = 11.2\ L_m^{3.04}$ which applies to fusiform

167 fishes (Froese et al. 2014; see other relationships in Meyer-Vernet and Rospars 2016). When no

168 indication was provided in the papers, we searched the average mass (or length) of the species in

169 the scientific literature (for example, Bartholomew and Heinrich 1973; Byrne et al. 1988; Niven

170 and Scharlemann 2005, for insects; Falk-Petersen 1981, for shrimps) or in websites. We have not

171 considered in the analyses two T_F data for which the mass could not be found (lines 24 and 87 in

172 Table S2). Otherwise, all body masses and their references are given in Tables S1-S3.

173

174 2.3. *Temperature Effects*

175

176 In order to check the dependence of the time scales on temperature, we used (in the Discussion

177 section only) the Boltzmann-Arrhenius model from chemical reaction kinetics, which holds

178 approximately for metabolic and locomotor rates (e.g. Dell et al. 2011). This model yields

179 biological time scales inversely proportional to the Boltzmann factor, $\exp(-E/k_B\theta)$, where *E* is the

180 activation energy of the process studied (in joules), k_B, the Boltzmann constant, and θ, the

181 temperature (in kelvins). Thus, the corrected time scale T_0, at the reference temperature θ_0, of

182 time *T* measured at temperature θ is $T_0 = T \exp(qE/k_B)$, where $q = 1/\theta_0 - 1/\theta$. For all timescales,

183 we chose $\theta_0 = 20\ °C$ as reference and $E = 0.66$ eV, the mean activation energy observed in a wide

184   range of species and traits (Dell et al. 2001). In the special case of T_S, we also applied a finer

185   standardization procedure distinguishing defence or movement away from a stimulus, like startle

186   responses, and consumption or movement toward a stimulus (almost all other responses), whose

187   mean activation energies are $E = 0.4$ and 0.7 eV, respectively (Dell et al. 2001).

188

189   2.4. *Statistical Analyses*

190

191   Statistics were computed on either data T or their log-transform ($\log_{10} T$). In the main text, but not

192   in Supplementary material, all data (T and $\log_{10} T$) were averaged per species, counting

193   separately sperm cells (in T_L data, Table S3) and late developmental stages (for *Danio rerio* and

194   *Procambarus clarkii* in T_S data, Table S1). The data in each category (T_S, T_F and T_L) were

195   characterized by their medians and interquartile ranges IQR. Lognormal distributions were fitted

196   after determination of their parameters (mean μ and standard deviation σ) on log-transformed

197   data. However, for easier readability, μ in log units was converted in seconds in text and figures

198   (except in Supplementary material Tables S7-S10), as $\mu^* = 10^\mu$ (μ^* is the geometric mean and

199   median of the lognormal distribution fitted to data T). Similarly, σ was expressed as a

200   multiplicative standard deviation $\sigma^* = 10^\sigma$ (σ^*, like σ, is dimensionless; it determines the

201   asymmetry of the distribution, and the interval $[\mu^*/\sigma^*, \mu^*\sigma^*]$ covers a probability of 68.3 %, see

202   Limpert et al. 2001). The overall interval of variation in each timescale was expressed as the

203   percentiles 2.5 % and 97.5 %, which are less sensitive to outliers and sampling fluctuations than

204   the minimum and maximum; the ratio of these percentiles and its logarithm (denoted δT_{95})

205   estimate the multiplicative range including 95 % of values. Statistical distributions were

206   compared with the Kolmogorov-Smirnov test. Least-square regressions of $\log_{10} T_i$ against

207    $\log_{10} M$ and least-rectangle regressions of $\log_{10} T_L$ against $\log_{10} MSMR$ (Dagnelie 2011) were

208 calculated and given as scaling equations $T_i = T_0 M^\alpha$ in figures and their slope (also called scaling

209 exponent) α as 95 % confidence intervals in the text. Tables S7-S10 provide details of ANOVA

210 and multiple comparisons of means using Tukey-Kramer adjustment method. We used the

211 significance level 5 % in all tests. We performed all statistics with the Matlab Statistical Toolbox

212 (The Mathworks, Natick, USA).

213

214 3. EMPIRICAL RESULTS

215

216 3.1. *Statistical Distributions of Timescales and Comparisons*

217

218   Simple response times, T_S, extend from 2.5 ms in the escape behaviour of the calanoid

219 copepod *Undinula vulgaris* to 485 ms in the acoustic response of the white whale *Delphinapterus*

220 *leucas*, with median 24 ms and IQR 43 ms. The distribution is lognormal (Fig. S1A), with

221 geometric mean $\mu^* = 26$ ms and multiplicative standard deviation $\sigma^* = 3.26$. Critical fusion times

222 T_F range from 2.5 ms in the black fire beetle *Melanophila acuminata* to 250 ms in the crustacean

223 isopod *Booralana tricarinata*, with median 24 ms and IQR 27 ms. The distribution is lognormal

224 (Fig. S1C) with $\mu^* = 25$ ms and $\sigma^* = 2.14$. The times to move by one body length at maximum

225 speed T_L extend from 5 ms for a sea urchin to 2.8 s for a large spirochetes bacterium, with

226 median 71 ms and IQR 99 ms (Meyer-Vernet and Rospars 2016). The distribution is lognormal

227 with $\mu^* = 78$ ms and $\sigma^* = 2.73$ (Fig. S1B). Since most of the variability in the data comes from

228 the diversity of species, stimuli and measurement methods, such lognormal distributions are

229 expected if these factors act in a multiplicative way.

230   Figure 1 compares as boxplots the (log-transformed) timescales T_F, T_S and T_L. Their relative

231 position is indicated by the medians (central red lines). ANOVA and multiple comparisons of

232   means show that the sensory timescale T_F and the simple response time T_S are similar, whereas T_L

233   is significantly different and about three times longer (Table S7).

234

235   3.2. *Variation with Body Mass*

236

237   To study the dependence of simple response times on body mass M for the whole data set

238   encompassing life's major domains, we plotted the pairs (M, T_S) in log-log plots for 81 species

239   (Fig. 2), including microorganisms in the mass range 10^{-16} (bacterium) to 5×10^{-13} kg (green alga)

240   and multicellular organisms from 3×10^{-9} (spider) to 3860 kg (elephant). Fig. 2A distinguishes the

241   taxonomic groups whereas Fig. 2B distinguishes the types of responses. Overall, the mass M

242   varies by a factor of about 10^{20} whereas 95 % of the T_S values lie between 4.7×10^{-3} and 0.31 s

243   (Table 1, first line). Although very small, the slope of the regression line is significantly different

244   from zero (95 % confidence intervals [-0.065, -0.010], Table 2), but as shown in Table 1, this

245   effect results from the larger simple response times in single cells ($\mu^* = 129$ ms) than in

246   multicellular organisms ($\mu^* = 22$ ms). Since this difference is significant (Table S8c, first line,

247    $p < 10^{-3}$), the two groups must be studied separately. The scaling exponents α of the power law

248   regressions in both groups are not significantly different from zero with 95 % confidence

249   intervals $[-0.41, 0.49]$ for single cells and $[-0.01, 0.08]$ for multicellular organisms, whereas the

250   intercepts differ by more than one order of magnitude (Table 2 and Fig 2A).

251   Flicker fusion times T_F could only be measured in multicellular organisms. Therefore, the

252   body mass of the 106 species shown in Figure 3 only varies from 2×10^{-6} kg (fruit fly) to 354 kg

253   (sea turtle), representing over eight orders of magnitude, whereas 95 % of the T_F values lie

254   between 2.5×10^{-3} s and 0.25 s (Table 1). No effect of body mass on T_F could be evidenced, since

255   the power law regression is $T_F = 0.026 M^{\alpha}$ (Fig 3), with α in the 95 % CI $[-0.01, 0.06]$ (Table 2).

256   The times to move by one body length at maximum speed T_L (Meyer-Vernet and Rospars

257   2016, Fig. 4) concern 426 species including microorganisms from 10^{-16} kg (bacterium) to

258   1.3×10^{-8} kg (ciliate eukaryotic cell) and multicellular organisms from 10^{-9} (copepod) to 1.4×10^5

259   kg (blue whale). So, M varies by 21 orders of magnitude whereas 95 % of the T_L values lie

260   between 21×10^{-3} and 0.71 s. The times T_L in single cells ($\mu^* = 145$ ms) are twice longer and

261   more variable than in multicellular organisms ($\mu^* = 69$ ms), this difference being significant

262   (Table S8b, second line, $p < 10^{-8}$). In both groups T_L increases slightly with mass, since the 95 %

263   CI of the slope of the regression line α is [0.020, 0.14] for single cells and [0.028, 0.060] for

264   multicellular organisms (Table 2). However, the trend of the multicellular group results from the

265   largest vertebrates since for species under 50 kg the slope of the regression law α is not

266   significantly different from zero (95 % CI is [−0.030, 0.11] (Table 2).

267   Since the maximum metabolic rate of organisms affects their maximum speed (Meyer-Vernet

268   and Rospars 2016), we studied also the dependence of T_L on maximum specific metabolic rates

269   (MSMR) in 14 species of mammals for which both values were determined (Table S5). The slope

270   of the regression lines of MSMR against body mass (Fig. S6A) and of T_L against MSMR (Fig.

271   S6B) are not significantly different from 0 and −1 respectively, suggesting independence of

272   MSMR on mass and inverse dependence of T_L on MSMR.

273

274   4. DISCUSSION

275

276   4.1. *Variability and Mass Dependency of Timescales*

277

278   Over the whole mass range, the variabilities of the timescales expressed by the ranges including

279   95 % of the data (δT_{95}, Table 1), are so small compared to the mass ranges (δM, Table 2), that

280   their ratios are always less than one in a million ($10^{\delta T95}/10^{\delta M}$). Indeed, 95 % of the simple

281   response times T_S (Fig. 2), of the visual resolution times ($T_F = 1/CFF$, Fig. 3) and of the minimum

282   locomotor times T_L (Fig. 4) lie within less than a factor of ten, five and six respectively of their

283   geometric mean, whereas the mass varies by 20, 8, and 21 orders of magnitude for T_S, T_F and T_L

284   respectively. This is noteworthy, given the diversity of sensorimotor systems and the huge mass

285   range, and suggests that these times are strongly constrained by physics, as was previously

286   proposed for T_L. The small variation of the visual resolution times is remarkable, given the

287   variation in spatiotemporal optical quality with eye size, which is correlated to body size (e.g.

288   Currea et al. 2018), and the large diversity of visual systems (e.g. Fernald 2000) and of strategies

289   of spatiotemporal summations. Although CFF is unrivaled to quantify the ability of an organism

290   to track a moving object, whether it is representative of other sensory systems is an open question

291   for further investigation. However, as suggested by a few reports (for example in olfaction,

292   Rumbo and Kaissling 1989, Lemon and Getz 1997, Smear et al. 2011, Jacob et al. 2017),

293   temporal resolution might reflect properties common to diverse neural networks rather than

294   specificities of the receptors (Butts et al. 2007, Panzeri et al. 2010) and, hence, be similar in the

295   visual and other sensory systems.

296   Most of the overall variability results from variations at smaller mass ranges. Within uni- and

297   multi-cellular organisms considered separately, the mass-scaling exponents are not significantly

298   different from zero or result from a small-scale trend (T_L in large metazoans), so that the T_L

299   (small) mass dependency in single cells appears as an exception that will need further data to be

300   interpreted. For T_S and T_L, differences between single cells and metazoans contribute to the

301   overall variability. The twice longer geometric mean of T_L in single cells (Table 1) is well

302   documented ($n = 70$ species) but the six times longer one of T_S ($n = 7$) should be confirmed on a

303   larger sample.

304   Although outside the scope of this paper, we examined narrower mass ranges, i.e. groups of

305   related species of the same class (or kingdom in microorganisms) including more than three

306   species (Fig. S3, S4, S5 and Table S6). For most groups, the mass scaling exponents are positive

307   with intercepts decreasing with mass, so that all the data still lie in a relatively narrow range, as

308   found previously for the mass specific metabolism (Makarieva et al. 2008, Hatton 2019) and its

309   maximum value (Makarieva et al. 2005). For simple response times T_S, the only exponent that

310   reaches statistical significance is that of mammals (Fig. S3) where the trend explains 42% of the

311   variance and agrees with previous studies (section 4.3). Although not significant, the trend in

312   bacteria stands out owing to the proportion of variance it explains (81 %) and its steep slope

313   ($\alpha = 0.66$) which agrees with first-principle derivations (section 5). For the flicker fusion time, the

314   mass exponent of the small-scale regressions are not significantly different from zero. Finally, for

315   the minimum time to move by one body length, the positive mass scaling exponent of mammals

316   stems from large masses (the inflection point near 50 kg is apparent in Fig. 4), as noted and

317   interpreted by Meyer-Vernet and Rospars (2016); we shall return to this point in section 5.

318

319   4.2. *Possible Errors Resulting from Biological, Methodological and Experimental Factors*

320

321   Are our data and analyses adequate for supporting our conclusion that the simple response time

322   T_S lies within less than a factor of ten from the mean for organisms varying by more than 20

323   orders of magnitude in mass, as previously shown for the minimum time to move by one body

324   length T_L (Meyer-Vernet and Rospars 2016)? That a similar finding holds for T_F over the smaller

325   10^8-fold mass range for which this time could be measured? And that these time scales display

326 small or no systematic variation with body mass in uni- and in multicellular organisms? Several

327 criticisms could be raised.

328   First, one could object that the diversity of organisms, of sensory and motor mechanisms, and

329 of experimental procedures hides any trend in the data. However, it is unlikely that the restriction

330 to more homogeneous data would reveal trends presently hidden because the smaller size of

331 samples would decrease the statistical significance. On the contrary, the diversity of species,

332 measurements and systems is indispensable to estimate reliably the variability and mean of the

333 timescales, independently of the specializations and limitations of taxa and systems. Our aim is to

334 transcend mass scalings holding within groups by considering large ranges of mass and

335 taxonomic groups.

336   Second, the evolution of different traits is correlated throughout a phylogenetic lineage so that

337 species values do not represent statistically independent data (Felsenstein 1985). This leads to

338 overestimation of degrees of freedom, which artificially narrows confidence intervals. Our major

339 finding that timescales lie within close bounds and that for unicellular (for T_S) and multicellular

340 organisms (for all timescales) they do not significantly depend on mass would not be adversely

341 affected by any widening of confidence intervals (on the contrary for T_L in single cells) and is

342 therefore impervious to this criticism.

343   A third possible objection is that several experimental factors affecting the measurements have

344 not been considered explicitly. The electrical or behavioural measurement methods play a minor

345 role and correcting them would have practically no effect (Fig. S2 and Table S10 show that their

346 difference is not significant). However, the effect of temperature, which is an important

347 determinant of metabolism and behaviour, should be checked. We thus studied how correcting

348 the time scales of ectotherms to a standard temperature $\theta_0 = 20\ °C$ would change our results (see

349 Methods). First, the temperature being unknown in several measurements, we considered the

350   worst-case scenario assuming that short time scales ($T < \mu^*$) were measured at 10 °C, and would

351   thus be still shorter if they had been measured at θ_0, and that long time scales ($T \geq \mu^*$) were

352   measured at 30 °C, these two temperatures being close to the extremes in our data (Fig. S7A). For

353   this preliminary test, we used the mean activation energy $E = 0.66$ eV observed in a wide range

354   of species and traits (Dell et al. 2001), and studied how the percentage of timescales lying outside

355   the range [$\mu^*/10$, $\mu^* \times 10$] would be affected by temperature in this worst-case scenario. For all

356   timescales, this percentage is less than 3 % without standardization (Table S11a) and less than

357   10 % with standardization (Table S11b), except for T_S where it is 5 % and 22 % respectively.

358   Next, noting the greater sensitivity of T_S, we applied a finer standardization procedure to this

359   timescale, for which the temperature is known in 72 % of our data for ectothermic species, based

360   on the different mean activation energies of movements away from and toward a stimulus (see

361   Methods). This procedure leads to no significant change neither in the distribution of T_S values

362   (Fig. S7B) nor in the number of species beyond the limits (it remains the same, i. e. four, Fig.

363   S7). This indicates that our results in mean, variability and overall trend are robust with respect to

364   temperature.

365

366   4.3. *Comparison with Previous Work*

367

368   Several studies across a wide range of mass and life forms have found organisms' properties to

369   lie in a relatively narrow range, without mass scaling across groups, despite the size scaling

370   observed within groups. This is the case for the mass-specific metabolic rate (Makarieva et al.

371   2008, Hatton et al. 2019), its maximum value per unit of active mass (Makarieva et al. 2005), the

372   cross-section-specific forces exerted by muscles and molecular motors (Marden and Allen 2002,

373   Marden 2005, Rospars and Meyer-Vernet 2016), and the minimum time to move by one body

374   length $T_L = L/V_{max}$ (McMahon and Bonner 1983, Meyer-Vernet and Rospars 2015, 2016).

375   However, for the simple response time T_S and the critical flicker fusion time T_F, previous

376   studies concern only relatively small mass ranges and we have included these data. The mass

377   scaling of sensorimotor delays has been studied by More and Donelan (2018) in the particular

378   case of the stretch reflex − a monosynaptic reflex that governs the fastest neural response to

379   peripheral stimuli in terrestrial mammals, with a determination of the different components and a

380   comparison with stance and stride durations. In our T_S sample, we have used the sum of these

381   components except the force generation delay (time between force onset and peak), in coherence

382   with the rest of our data, for which the response is measured by the onset of force production or

383   the onset of movement (which can begin before the production of peak force). These data points

384   lie within the range of our general data set T_S for multicellular organisms, where the nerve

385   conduction delay is expected to be mainly responsible for the increase of T_S shown in figure 2 at

386   large mass. Indeed, the increase in nerve conduction speed due to increase in fibre diameter and

387   to myelination is too moderate to compensate for the increase in distance of conduction, because

388   of the trade-off between responsiveness and compactness (Castelfranco and Hartline 2016),

389   resolution (More et al. 2013), and energy cost (Perge et al. 2012). Let us compare the nerve

390   conduction delay estimated by More and Donelan (2018) $T_{cond} = 5.3\ M^{0.3}$ ms to the geometric

391   mean ($T_S = 22$ ms) that we find for multicellular species (Table 1). This yields

392    $T_{cond}/T_S = 0.24\ M^{0.3}$, which shows that the conduction delay becomes important only for large M,

393   although even for the largest mammal studied (the elephant), T_S is only four times larger than its

394   average value.

395

396   5. QUANTITATIVE INTERPRETATIONS FROM FIRST PRINCIPLES

397

398   The variation of the simple response time, as well as the other time scales studied here, by less

399   than a factor of ten around their mean for organisms so diverse in structure and size suggests that

400   it may be determined by basic constraints set by the universal properties of living matter. We will

401   thus derive first-principle estimates, trying to capture the essential processes at play, whereas

402   neglecting specific details that should be considered in scaling studies over narrow ranges of

403   mass and taxa. Such simple analytic calculations are expected to yield only order-of-magnitude

404   results, that is to within a 10-fold or so accuracy, similar to the variability of the time scales in

405   our data, in the line of the so-called "Fermi problems" or of Weisskopf's physics courses

406   (Weisskopf 1975, 1989).

407

408   5.1. *Simple Response Time*

409

410   Consider first the simple response time T_S of microorganisms. It includes the transmission delay

411   from the sensor(s) receiving external stimuli to the motor apparatus producing the response by

412   regulating the swimming behaviour. A basic process is the transport of a signalling molecule

413   through the cytoplasm (e.g. Bitbol and Wingreen 2015) via diffusion (e.g., Purcell 1977,

414   Dusenberry 2009). In water, of viscosity $\eta \simeq 10^{-3}$ kg m^{-1} s^{-1}, a sphere of diameter d at

415   temperature θ has a diffusion coefficient $D = k_B \theta/(3\pi\eta d)$, where k_B is Boltzmann constant.

416   Signalling molecules are small proteins of typical size $d \simeq 3$ nm, like the key signalling protein

417   CheY (Bren and Eisenbach 2000), yielding a diffusion coefficient in water $D \simeq 150$ µm^2/s.

418   Assuming that the crowding of the cytoplasm decreases D by one order of magnitude (e.g. Dill et

419   al. 2011, Mika and Poolman 2011) and that the sensor-to-motor distance equals the organism's

420   length L, we find the three-dimensional diffusion time $L^2/6D$

421          $\tau_{\text{dif}} \simeq 10 \, L_{\mu m}^2$ ms.   (1)

422   This timescale is the minimum response time T_S of a microorganism of size L if information is

423   transmitted through the cytoplasm by diffusion of signalling proteins, which is the most basic

424   process. With $L \propto M^{1/3}$, this would yield a mass variation $T_S \propto M^{2/3}$, as observed for bacteria (see

425   the leftmost regression line in Figure S3 with slope $\alpha = 0.66$, as given in Table S5). The median

426   mass of a bacterium of length L being $M \simeq (3.3L)^3$ (Meyer-Vernet and Rospars 2016), the length

427   of a bacterium of mass 10^{-15} kg (μ_M*, Table S6) is $L \simeq 3$ μm. We deduce from Eq. (1) $T_S = 90$

428   ms, which agrees to better than a factor of two with the empirical value for bacteria ($\mu^* = 144$ ms

429   in Table S5) and is close to the response time given by their regression line ($T_S = 100$ ms for

430     $M = 10^{-15}$ kg, Table S6).

431   Consider now multicellular organisms. For most of them, the responses are mediated by

432   conduction of information via electric pulses propagating through neurons, whose membrane

433   regulates the permeation of ions via an insulating lipid bilayer and proteins. The proteins act as

434   active ion channels and pumps and the lipid bilayer acts as a capacitance that enables charges to

435   accumulate and produce a potential across it. Biological membranes are also involved in sense

436   organs, via the concentration gradients they enable which produce active transport, whereas ion

437   channels play an essential role in signal transduction (Martinac and Cox 2016). The role of ions

438   to alter charge and thus protein conformation is essential in signal transduction in both uni- and

439   multicellular organisms (Clapham 2007). For example, paramecia use Ca^{2+} ions and show

440   dynamic changes in the electrical properties of their membrane in response to stimuli, as do

441   neurons, and the structures of their receptors are similar to those of vertebrates (e.g. Maegawa

442   2017).

443   A tentative first principle estimate of T_S can be obtained from the inverse of the number of

444   action potentials sent along an axon per second, since this is the shortest possible time to send a

445   bit of information along an axon. Let us first evaluate the cost of generating an action potential U

446   per surface S of membrane, of width a and dielectric constant ε_m, so that the capacitance is

447        $C \simeq \varepsilon_0 \, \varepsilon_m \, S/a,$ (2)

448   where ε_0 is vacuum permittivity. With the electric charge across the membrane CU, of energy

449   CU^2, the cost of an action potential is obtained from (2) as $\varepsilon_0 \, \varepsilon_m \, S \, U^2/a$, which agrees with values

450   in the literature (Aiello 2000). Using two biological properties common to living matter: the mass

451   density $\rho \simeq 10^3$ kg/m^3 and the maximum metabolic rate per unit mass of active tissue

452    $b_M \simeq 2\times10^3$ W/kg (Makarieva et al. 2005), the maximum power available to this surface S of

453   membrane of mass $\rho a S$ is

454        $b_M \, \rho a S$ (3)

455   Dividing this maximum power by the cost of an action potential estimated above and using the

456   energy corresponding to one monovalent ion crossing the membrane $eU \simeq W_0$, where

457    $e = 1.6\times10^{-19}$ C is the electron charge and W_0 is the energy released by one ATP molecule, we

458   deduce the maximum number of action potentials per unit time, whose inverse yields

459        $T_S \simeq \varepsilon_0\varepsilon_m W_0^2/(\rho b_M \, e^2 a^2)$ (4)

460   Substituting the typical dielectric constant of lipids $\varepsilon_m \simeq 2$, a membrane width $a \simeq 6$ nm – similar

461   to the typical protein size (e.g. Erickson 2009), the above value of b_M, and the first-principles

462   relation (Meyer-Vernet and Rospars 2016)

463        $W_0 \simeq e^2/(4\pi\varepsilon_0 a)$ (5)

464   we obtain $T_S \simeq 14$ ms, close to the empirical mean simple response time T_S of metazoans (22

465   ms).

466

467   5.2. *Flicker Fusion Time*

468

469   Let us now estimate the timescale T_F, assuming that it is limited by the membrane time constant

470   τ_m. For a surface S of membrane of width a and resistivity r_m, the electrical resistance is

471    $R = r_m a/S$ and the capacitance is given by (2), so that the time constant $\tau_m = RC$ is given by

472        $\tau_m = r_m \varepsilon_0 \varepsilon_m.$ (6)

473   To estimate a basic value for the resistivity r_m, independent on the details of the system, we

474   consider again energy constraints. In an electrical circuit of resistance R, submitted to the

475   potential difference U, the power is U^2/R. Using the maximum power available (3), we deduce

476   the resistance $R \simeq U^2/(b_M \rho\, a\, S)$, whence the resistivity $r_m \simeq U^2/(\rho b_M a^2)$. Using again the order

477   of magnitude $U \simeq W_0/e$, we deduce τ_m, which yields the flicker fusion time $T_F \simeq \tau_m$ (reflecting the

478   ability of the membrane to resolve a time-varying signal)

479        $T_F \simeq \varepsilon_0 \varepsilon_m W_0^2/(\rho b_M e^2 a^2) \simeq T_S \simeq 14$ ms   (7)

480   close to the empirical value of T_F (25 ms), and in agreement with our empirical result $T_F \simeq T_S$.

481   The absence of significant increase of T_F for the largest masses (Fig. 3), contrary to what is

482   observed for T_S (Fig. 2) suggests that the signal conduction time and hence the organism length L

483   plays a minor role in T_F, contrary to T_S.

484

485   5.3. *Minimum Locomotion Time*

486

487   An order of magnitude estimate of the minimum time to move by one body length $T_L = L/V_{max}$

488   was derived by Meyer-Vernet and Rospars (2016) from the invariance over the whole domain of

489   life of the force per cross-sectional area exerted by molecular motors and muscles ($f \simeq W_0/a^3 \simeq$

490   2×10^5 N/m², Rospars and Meyer-Vernet 2016), and the two basic quantities considered above,

491   mass density ρ and mass-specific (per unit mass of active tissue) metabolic rate at maximum

492   activity b_M. The maximum speed was estimated as $V_{max} \simeq L \rho b_M / f$ for swimming and running

493   organisms (including microorganisms) of length L satisfying $L \lesssim (f / \rho)^{3/2}/b_M \simeq 1.4$ m −

494   corresponding roughly to $M \simeq 50$ kg (Meyer-Vernet and Rospars 2016). This yields $T_L \simeq L/V_{max}$,

495   the minimum time to move by L

496   $$T_L \simeq f / (\rho \, b_M) \simeq W_0 /(\rho \, b_M \, a^3) \simeq 100 \text{ ms} \qquad (8)$$

497   for $M \lesssim 50$ kg, which agrees to better than a factor of two with the empirical value (59 ms,

498   geometric mean of T_L for all organisms of mass $M < 50$ kg, Table 1). The increase in T_L observed

499   for larger organisms (Fig. 4) has been interpreted by dynamic constraints, yielding

500   $$T_L \simeq L \, (\rho/f)^{1/2} \qquad (9)$$

501   (Meyer-Vernet and Rospars 2016), in agreement with the known maximum speed of about 15

502   m/s (e.g. McMahon and Bonner 1983, Garland, 1983, Iriarte-Diaz 2002).

503   It is interesting to note that our estimates of the minimum times for response (4), for vision

504   (7), and for moving by one body length (8) all yield timescales proportional to the inverse of the

505   maximum mass-specific metabolic rate (per unit of active mass). This suggests that, since the

506   metabolic rate varies with mass within groups of related species, these time scales may depend

507   not only on body mass within groups of related species but also on metabolic rates. This is shown

508   for T_L in mammals (Fig. S6B), which is inversely proportional to the maximum mass-specific

509   metabolic rate, as expected from (8) if the proportion of active tissue in the body mass does not

510   vary in the range considered in the regression.

511   Finally, it is noteworthy that Eqs. (4), (5) and (8) yield $T_L/T_S \simeq 4\pi/\varepsilon_m \simeq 6$ in order of

512   magnitude, to be compared to the empirical ratio $T_L/T_S = 78/26 = 3$, suggesting that fast reacting

513   species are also fast moving.

514

515   6. CONCLUSIONS

516

517   We have shown that across the whole of mobile life, from bacteria to large vertebrates, the simple

518   response time T_S lies in a relatively narrow range, with 95 % of species reacting in a time that

519   differs by less than one order of magnitude from the mean, in striking contrast to the 20 orders of

520   magnitude difference in body mass. The simple response time does not display significant scaling

521   with body mass across groups in unicellular organisms nor in multicellular ones, although it is

522   almost six times larger in the former life form. The absence of large-scale trend does not preclude

523   – and is indeed compatible with various scalings valid in narrower ranges of size and taxa, as is

524   known for the specific metabolic rate. However, within narrow ranges, the detailed characteristics

525   of the organisms must be considered and it is only on larger scales that these variations can be

526   transcended.

527   This simple response time T_S is close to a well-studied sensory timescale (the inverse of the

528   critical flicker fusion frequency for vision) T_F, and is a few times smaller than the minimum time

529   to move by one body length T_L, with all time scales lying in a relatively narrow range. Since this

530   narrow range suggests that these time scales may be strongly constrained by physics and basic

531   properties of life, independently of the structure or mass of the organism, we have performed

532   tentative simple estimates of T_S and T_F based on fundamental physicochemical constants and

533   basic properties common to motile organisms.

534   It is fair to note that the agreement between these simple estimates of minimum time scales

535   (for sensing, for reacting and for moving) and the measurements is only indicative of the

536   dominant constraints in play (e.g. Phillips and Milo 2009), since several mechanisms may be

537   operating in parallel. For example, one tenth of second is in the middle of the range of protein

538   folding time scales, which however spans six orders of magnitude (e.g. Lane and Pande 2013)

539   and close to the maximal turn-over rate of the most abundant enzyme in the biosphere (e.g.

540   Flamholz et al. 2019). The relation $T_S \simeq T_F < T_L$ found from the data (Fig. 1) and tentatively

541   interpreted from first-principles, is reminiscent of symmorphosis (Weibel et al. 1991) and

542   expected to be favoured by evolution since it is indicative of an optimum state. Indeed, if $T_S < T_F$

543   the sensory resolution would be in excess over motor control whereas if $T_S > T_F$ the response

544   would be limited by sensory performance, so that in both cases, at least one component of the

545   nervous system would be out of tune and wasting energy or space (Laughlin 2001). Likewise, the

546   evolution is expected to favour organisms for which the sensory and response organs act fast

547   enough with respect to their moving performances. It is noteworthy that since the first-principle

548   estimate (8) of T_L holds for both uni- and multi-cellular organisms (Meyer-Vernet and Rospars

549   2016), the estimate (1) of the minimal response time T_S yields a maximal length L of a few

550   micrometres in order to ensure $T_S \leq T_L$ when the response is mediated by diffusion, as observed

551   for bacteria

552   These preliminary results encourage further research on the response times of mobile

553   organisms and their fundamental bases. They might also possibly be used to infer properties of

554   extinct species since the reconstructed speed (e.g. Hutchinson and Garcia 2002) and size (e.g.

555 Hutchinson et al. 2011) of the giant dinosaur *Tyrannosaurus rex* yield a time to move by one

556 body length $T_L \simeq 1$ s for a mass $M \simeq 10^4$ kg, which is close to the value expected from (9) and

557 would put *Tyrannosaurus rex* in the middle of the data of extent animals of this size in figure 4.

558

559   *Ethical Statement*

560   The present article is based on a meta-analysis. No live animals were used.

561

562   *Data Accessibility*

563   The datasets supporting the article are included in the Supplementary Material.

564

565   *Competing Interests*

566   We have no competing interests.

567

568   *Author's Contributions*

569   J.-P.R. and N.M.-V. each made significant and substantial contributions to this study in terms of

570   the conception, design, data collection and interpretation of results, as well as preparing the

571   manuscript. J.-P.R. contributed primarily to the statistical analyses and N.M.-V. to the physical

572   analyses.

573

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733

734 TABLE 1. Summary statistics of timescales (in ms) for unicellular, multicellular and all species

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Timescale	n	min	max	$Q_{2.5}$	$Q_{97.5}$	r_{95}	δT_{95}	med	IQR	μ^*	s^*	out$_{95}$	out$_{10}$
T_S all	81	2.5	485	4.7	311	66	1.82	24	43	26	3.26	4	4
T_S unicell	7	18.0	350	18.0	350	19	1.29	200	195	129	3.17	0	0
T_S multicell	74	2.5	485	4.7	238	51	1.71	23	35	22	2.93	4	3
T_S multic<50kg	68	2.5	240	4.6	148	32	1.51	18	28	19	2.64	4	1
T_F all multic	106	2.5	250	4.2	100	24	1.37	24	27	25	2.14	5	1
T_L all	427	5.3	2778	20.9	706	34	1.53	71	99	78	2.73	22	11
T_L unicell	70	5.3	2778	11.9	2778	234	2.37	123	213	145	3.86	2	9
T_L multicell	357	12.5	2525	22.3	567	25	1.41	61	82	69	2.40	18	3
T_L multic<50kg	300	12.5	657	21.5	408	19	1.28	50	61	59	2.22	14	3

750 Rows: T_S, simple response time; T_F, flicker fusion time; T_L, minimum time to move by one body

751 length.

752 Columns: n, number of species; minimum; maximum; $Q_{2.5}$, percentile 2.5 %; $Q_{97.5}$, percentile

753 97.5 %; r_{95}, ratio $Q_{97.5}/Q_{2.5}$ including 95 % values; $\delta T_{95} = \log_{10}(r_{25})$; med, median; IQR,

754 interquartile range; μ^*, geometric mean (ms); s^*, multiplicative standard deviation; out$_{95}$, number

755 of values outside $[Q_{2.5}, Q_{97.5}]$; out$_{10}$, number of values outside $[\mu^*/10, \mu^* \times 10]$.

756

757 TABLE 2. Dependence of timescales on body mass for unicellular, multicellular and all species

758 ---

	n	$\log_{10}T_0$	α	IC_1	IC_2	μ_M*	δM	r_α	δT_α	r^2	P	Sig
T_S all	81	−1.69	−0.033	−0.06	−0.01	−3.10	19.59	0.2	−0.64	7	0.02	1
T_S unicell	7	−0.35	0.038	−0.41	0.49	−14.17	3.70	1.4	0.14	1	0.83	0
T_S multicell	74	−1.58	0.036	−0.01	0.08	−2.05	12.11	2.7	0.44	3	0.12	0
T_S multic<50kg	68	−1.77	−0.024	−0.08	0.03	−2.45	9.89	0.6	−0.24	1	0.36	0
T_F all multic	106	−1.57	0.023	−0.01	0.06	−1.93	8.25	1.6	0.19	2	0.19	0
T_L all	427	−1.13	−0.010	−0.02	−0.00	−2.86	21.05	0.6	−0.20	1	0.03	1
T_L unicell	70	0.10	0.078	0.02	0.14	−12.01	8.01	4.2	0.63	10	0.01	1
T_L multicel	357	−1.11	0.044	0.03	0.06	−1.06	14.15	4.2	0.62	7	0.00	1
T_L multic<50kg	300	−1.25	−0.010	−0.03	0.01	−1.72	10.70	0.8	−0.10	0	0.34	0

772 ---

773 Rows: same as in Table 1.

774 Columns: n, number of species; $\log_{10}T_0$, intercept of least square regression line, $\log_{10} T = \log_{10}T_0$

775 $+ \alpha \log_{10} M$; α, allometric coefficient; [IC_1, IC_2], 95% confidence intervals of slope α; μ_M*, mean

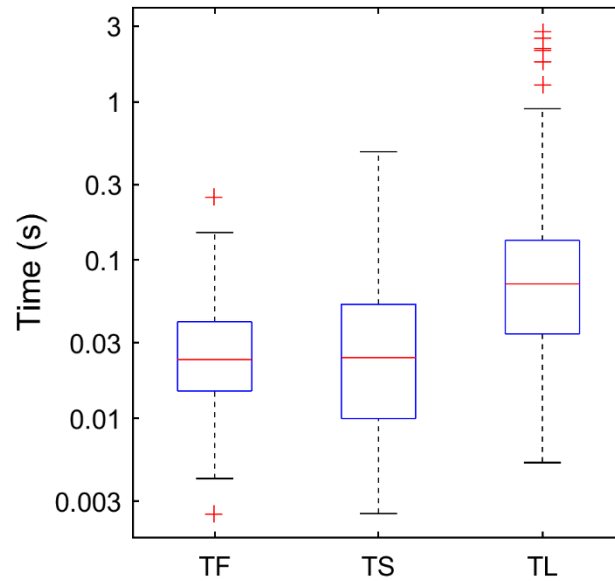776 $\log_{10}M$; δM, mass range of the category, $\delta M = \log_{10}(M_{max}/M_{min})$, with M_{max} and M_{min} masses of

777 heaviest and lightest species in the category; r_α, fitted ratio T_{max}/T_{min} with $T_{max} = T_0(M_{max})^\alpha$ and

778 $T_{min} = T_0(M_{min})^\alpha$; $\delta T_\alpha = \log_{10} r_\alpha$; r^2, coefficient of determination (percent); P, p-value of test of

779 slope $\alpha = 0$; Sig, slope α of regression line significantly different from zero (1) or not (0).

780

781

782   **Figure 1.** Boxplots of log-transformed flicker fusion times T_F, simple response times T_S, and

783   times to move by one body length at maximum speed T_L. The boxes extend from the lower

784   quartile to the upper quartile values with the medians (red line) in between. The whiskers extend

785   to the most extreme data values within 1.5×IQR. Outliers (red crosses) are values beyond the end

786   of the upper whiskers. ANOVA and multiple comparisons of means (Supplementary material,

787   Table S7): $T_F = T_S \neq T_L$.

788

789
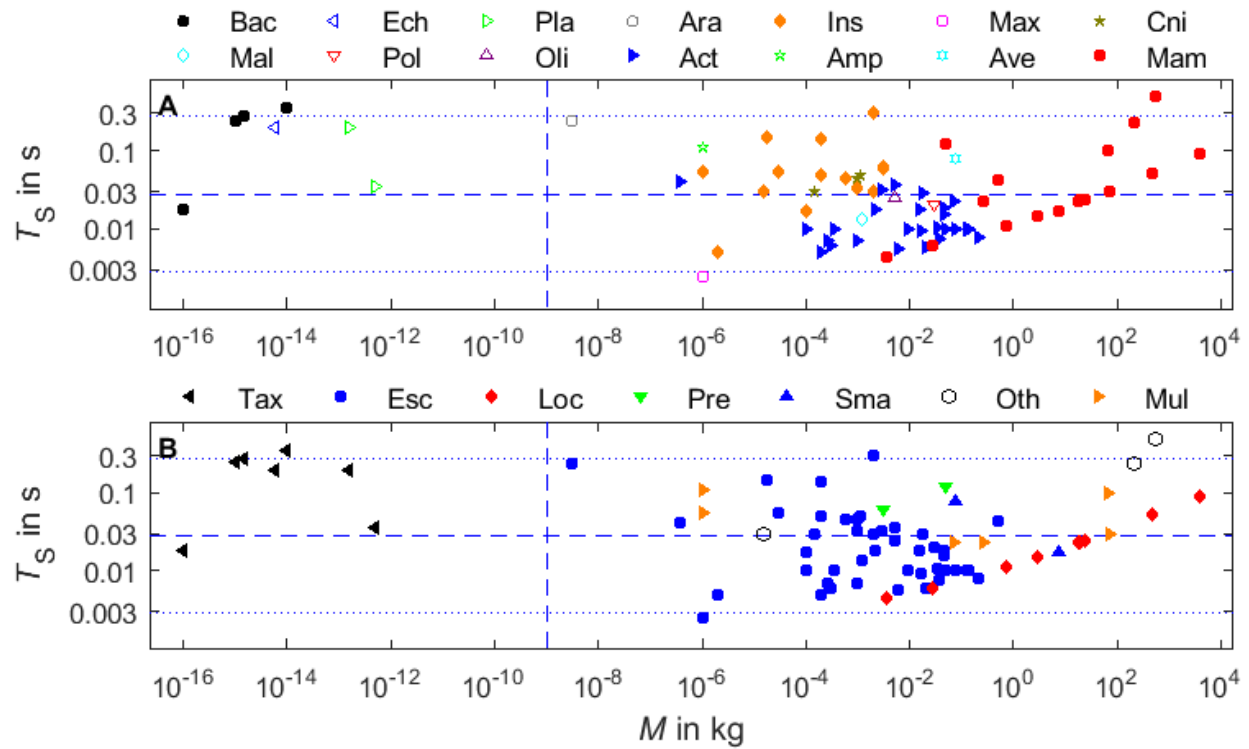
Figure 2. Simple response times T_S versus cell or body mass M ($n = 81$). For clarity, the scale on

the y-axis is 1.5 times larger than on the x-axis .

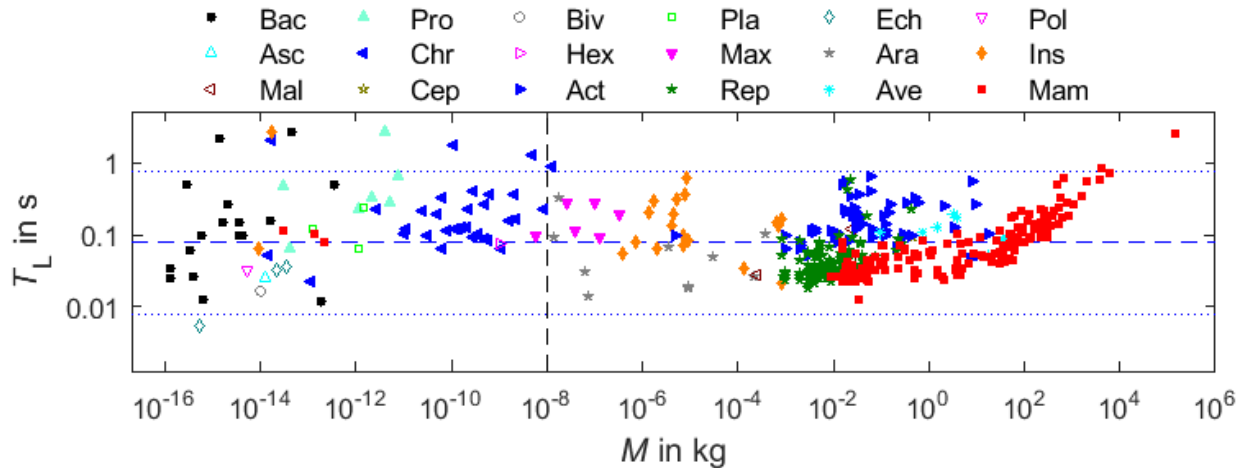**A**. Taxonomic groups. Groups with three species or less shown as empty symbols, other groups

as filled symbols. Bacteria (Bac, $n = 4$), Echinodermata (Ech, 1, sperm), Planta (Pla, 2),

Arachnida (Ara, 1), Insecta (Ins, 16), Hexanauplia (Hex, 1; copepods), Cnidaria (Cni, 3),

Malacostraca (Mal, 2; crustaceans), Polychaeta (Pol, 1; bristle annelids), Oligochaeta (Oli, 1;

earthworms), Actinopterygii (Act, 28; cartilaginous fishes), Amphibia (Amp, 1), Aves (Ave, 1;

birds), Mammalia (Mam, 18). The horizontal dashed line is the geometric mean μ^* (26 ms) with

values larger and smaller by one order of magnitude dotted. Vertical dashed line separates

unicellular from multicellular organisms. Intermediate-scale regression laws for, from left to

right, single cells (solid black line), multicellular organisms above 50 kg excluded (dashed black

line) and included (solid black line). Slopes not significantly different from zero.

B. Types of response. Species tested for a single type of response shown in filled symbols: cell

chemotaxis and phototaxis (Tax, $n = 7$), startle with escape (Esc, 46), sensory control of

locomotion (Loc, 11), predatory movement (Pre, 6), small movement in startle of birds and

mammals (Sma, 2), other behaviour (Oth, 3; see Table S1). Species tested for two or more types

of response (empty symbol, Mul, 6). Dashed and dotted horizontal lines as in A.
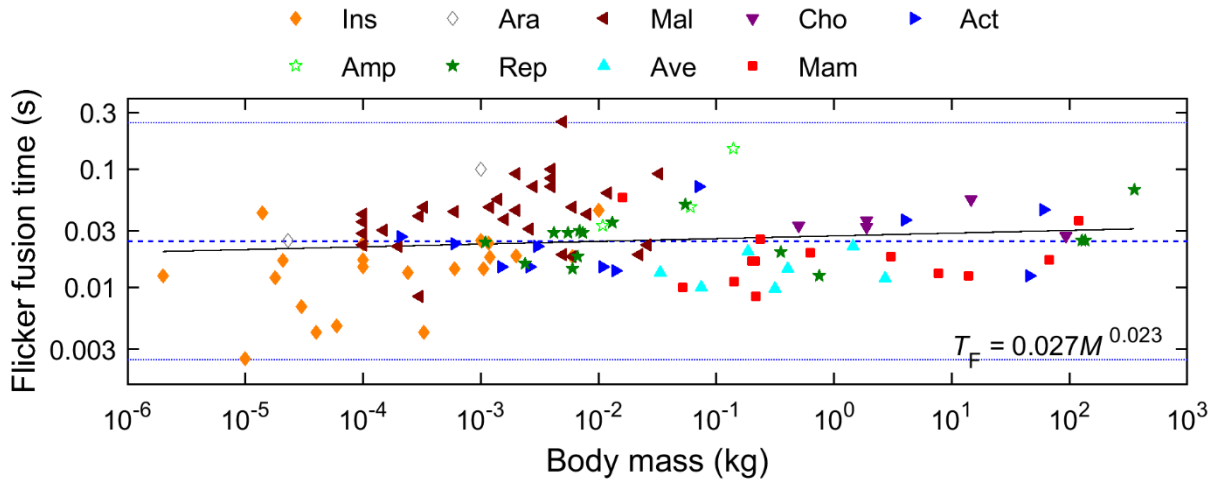
Figure 3. Flicker fusion times T_F versus body mass M ($n = 106$) according to taxonomic groups, shown as colour of empty and filled symbols as in Fig. 2. Arachnida (Ara, $n = 2$), Insecta (Ins, 21), Malacostraca (Mal, 29; crustaceans), Cho (Chondrichthyes, 5; cartilaginous fishes), Actinopterygii (Act, 11; ray-finned fishes), Amphibia (Amp, 3), Reptilia (Rep, 15), Aves (Ave, 7; birds), Mammalia (Mam, 13). The horizontal dashed line is the geometric mean μ^* (25 ms) with values larger and smaller by one order of magnitude dotted. Scaling regression law in inset. Slope not significantly different from zero.

816

Figure 4. Times to move by one body length at maximum speed T_L versus cell or body mass ($n = 426$) according to taxonomic groups. For clarity, the scale on the y-axis is 1.5 times larger than on the x-axis. Groups with three species or less shown as empty symbols, other groups as filled symbols. Bacteria (Bac, $n = 17$), Protozoa (Pro, 7; flagellates), Bivalvia (Biv, 1, sperm), Planta (Pla, 3), Echinodermata (Ech, 3, sperm), Polychaeta (Pol, 1, sperm; bristle annelids), Ascidiacea (Asc, 1, sperm; sea squirts), Chromista (Chr, 32; ciliates), Hexanauplia (Hex, 6; copepods), Arachnida (Ara, 10), Insecta (Ins, 20; 2 sperm), Malacostraca (Mal, 3; crustaceans), Cephalopoda (Cep, 1), Actinopterygii (Act, 55; cartilaginous fishes), Reptilia (Rep, 96), Aves (Ave, 9; birds), Mammalia (Mam, 161; 3 sperm). The horizontal dashed line is the geometric mean μ^* (78 ms) with values larger and smaller by one order of magnitude dotted. Vertical dashed line approximately separates unicellular and multicellular organisms. Intermediate-scale regression laws in inset as in Fig. 2. Slopes significantly different from zero, except for multicellular organisms under 50 kg.