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# How fast do mobile organisms respond to stimuli? Response times from bacteria to elephants and whales

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► **To cite this version:**

Jean-Pierre Rospars, Nicole Meyer-Vernet. How fast do mobile organisms respond to stimuli? Response times from bacteria to elephants and whales. *Physical Biology*, 2021, 18 (2), 10.1088/1478-3975/abcd88 . hal-03171698

**HAL Id: hal-03171698**

**<https://hal.sorbonne-universite.fr/hal-03171698>**

Submitted on 17 Mar 2021

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3 1 HOW FAST DO MOBILE ORGANISMS RESPOND TO STIMULI?  
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6 2 RESPONSE TIMES FROM BACTERIA TO ELEPHANTS AND WHALES  
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33  
34 14 Manuscript length: 9800 words (title page, summary and statements not included)  
35

36 15 Number of figures: 4.  
37

38 16 Number of tables: 2.  
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40 17 Supplementary material: yes.  
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43 18  
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45 19 Keywords: response time, startle response, locomotion, biophysical modelling, biological scaling.  
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54 Published in Phys. Biol. 18 (2021) 026002

<https://doi.org/10.1088/1478-3975/abcd88>

## 22 SUMMARY

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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

The concept of timescale is fundamental in science. An important timescale in biology is the minimum response time of mobile organisms to a dynamic environment. When an animal suddenly encounters a prominent event such as a prey, a predator or an obstacle, it must react fast enough, albeit not faster than necessary, in order not to sacrifice accuracy or waste the energy or space dedicated to its sensory systems (e.g. Attwell and Laughlin 2001). For a response to be fast enough, the information that produced the response should not be outdated (e.g. Spence 2009), which requires in particular that the response time does not exceed the movement duration and that the animal position has not changed much. For animals moving with legs, the response time is often compared to the stance or step duration (e.g. More et al. 2018); however, for animals not equipped with legs, a more general time scale for comparison with the minimum response time is the minimum time to move by one body length, that is the ratio of body length to maximum speed.

The maximum speed of terrestrial and aquatic organisms has been found to be roughly proportional to their body length, from bacteria to large vertebrates (Bonner 1965, McMahon and Bonner 1983), contrary to the preferred speed which is subjected to different constraints (e.g. Bejan and Marden 2006). These results, later confirmed with a large data set, imply that the time to move by one body length at maximum speed lies in a narrow range around one tenth of second within a factor of ten, for running and swimming organisms of mass varying by  $10^{20}$ -fold in body mass. The ubiquity of this minimum locomotion time scale, holding for so different organisms' structures and sizes, whereas characteristic biological timescales cover more than 12 orders of magnitude (e. g. Shamir et al. 2016), suggests that it is bounded by universal constraints, and led Meyer-Vernet and Rospars (2015, 2016) to propose a tentative interpretation

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3 64 based on the mass density of living organisms, the maximum specific tension exerted by  
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5 65 molecular motors and muscles (Rospars and Meyer-Vernet 2016) and the maximum mass  
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7 66 specific metabolic rate (Weibel and Hoppeler 2005, Glazier 2014, Makarieva et al. 2005), which  
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9 67 constrain the maximum speed and remain within close bounds for all moving organisms.  
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12 68 The question therefore arises of whether a similar result could hold for the minimum time to  
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14 69 react to stimuli. The scaling of sensorimotor delays with body mass in relation to movement  
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16 70 duration has been studied by More and Donelan (2018) for the stretch reflex in terrestrial  
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18 71 mammals, but there is no large-scale study of the minimum response time covering the entire  
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20 72 mass range of mobile species. We therefore collated data from the literature for the ‘simple  
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22 73 response time’, that is the time to detect the occurrence of a simple stimulus, as determined from  
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24 74 behavioural and electrophysiological measurements in various taxa from free-living cells to large  
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26 75 metazoans like sharks, turtles, and elephants, spanning 20 orders of magnitude in mass from  
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28 76  $10^{-16}$  to 3900 kg.  
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33 77 An important constraint to fast response is set by sensory limitations that affect the ability to  
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35 78 track fast moving objects such as prey or mates. These limitations have been studied in the case  
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37 79 of vision, using the critical flicker fusion frequency (CFF), defined as the frequency at which a  
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39 80 flickering light is indistinguishable from a continuous light (e.g. D’Eath 1998). The scaling of  
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41 81 this property with body mass and metabolism has been studied by Healy et al. (2013) for  
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43 82 vertebrates; we collated the corresponding characteristic time ( $1/\text{CFF}$ ) and extended the data to  
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45 83 compare it to the minimum response time.  
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49 84 Our aims are (i) to determine whether the minimum response time remains within close  
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51 85 bounds across the whole of mobile life despite the diversity of structures and mechanisms, (ii) to  
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53 86 compare it with the minimum sensory time-scale for vision (inverse of the critical flicker fusion  
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55 87 frequency) and to the minimum time to move by one body length, and (iii) to propose an  
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3 88 interpretation based on basic physicochemical and biological properties. Because the response  
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5 89 times of animals are expected to be hugely different from those of microorganisms, which are  
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8 90 subjected to very different constraints (e.g. Martens et al. 2015), we also investigate the  
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10 91 timescales separately for single cells and for metazoans.

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12 92 The empirical data are studied and discussed in sections 2 to 4. Section 5 proposes order-of-  
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14 93 magnitude interpretations based on fundamental physicochemical constants and basic properties  
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17 94 of life, with conclusions given in Section 6.

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## 20 21 96 2. MATERIAL AND METHODS

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### 25 26 98 2.1. *Data Collection*

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31 100 We define as “simple response time” ( $T_s$ ) the time to detect the occurrence of a simple and  
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33 101 sudden stimulus. These  $T_s$  are delays from the time at which the stimulus reaches the organism to  
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35 102 either the onset of movement – measured by behavioural methods (for example with high-speed  
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37 103 cinematography), or to muscle activation – measured by electrophysiological methods with direct  
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39 104 recordings from muscles (electromyogram EMG). Since our study concerns minimum response  
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42 105 times, it does not include the “discrimination (or identification) and choice response times” (e.g.  
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44 106 Luce 1991). In these complex tasks, the subject, whether animal or human, is presented with one  
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47 107 of several stimuli and has to respond to only one of them (discrimination, e.g. Blough 1978) or to  
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49 108 perform different responses depending on the stimulus presented (choice between stimuli, e.g.  
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51 109 Abraham et al. 2004). Likewise, for microorganisms, we only considered the response delay after  
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54 110 a stimulus (e.g. Block et al. 1982), which only involves internal time scales of the organisms and  
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56 111 is shorter than the time based on the comparison of different measurements, which depends on

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3 112 ambient conditions (e.g. Mitchell 1991). Thus, our definition of simple response times  $T_s$  being  
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5 113 based on the simplicity of the task and the stimulus does not take into account the length,  
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7 114 variability or underlying sensorimotor mechanisms of the response delays (Roeder 1963, Koch  
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9 115 1999, Herberholz and Marquart 2012, Sillar et al. 2016, Roberts et al. 2019). It avoids the  
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11 116 operational difficulty to implement these multiple criteria and insures a better representativeness  
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14 117 of the sample.

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17 118 We searched the Google Scholar database and extracted simple response times and other  
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19 119 relevant data (species names, stimuli, experimental conditions, etc.) published in refereed  
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21 120 journals. Our main objective being to investigate the interspecific variability, we kept all values  
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23 121 found for non-human species, but not for humans, for which we considered only a selection of  
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25 122 papers, either classical or illustrating the diversity of experimental paradigms. For a given species  
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27 123 and stimulus, we tabulated simple response times as the mean provided by the authors, or the  
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29 124 mean of the extremes when given as a range.

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33 125 Our  $T_s$  sample (Table S1) includes 175 measurements on 81 species. Behavioural ( $n = 134$ )  
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35 126 and electromyographic (EMG,  $n = 41$ ) measurements (column M in Table S1) are not  
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37 127 significantly different (Fig. S2A and Table S10); thus, we pooled them together in subsequent  
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39 128 analyses. The data belong to two main classes: startle and non-startle. “A startle response is an  
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41 129 abrupt response, often of relatively short latency, to a sudden stimulus that we believe to be both  
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43 130 unexpected and alarming (i.e., of high valence)” (Bullock 1984), so that threats that develop  
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45 131 gradually are excluded. Startle responses form a homogeneous class gathering the majority of  
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47 132 measurements (73 %) and of species (68 %, multicellular only). They may result in a large  
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49 133 movement translating the whole body (escape, called fast-start in fishes, 86 measurements on 50  
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51 134 species) or in small movements (called sometimes ‘eyelid, jaw, etc. reflex’ in birds and  
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55 135 mammals, depending on the muscle triggered, 42 measurements in five species). Non-startle

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3 136 responses (27 % of measurements on 32 % of species) include taxes (in single cells only), reflex  
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5 137 control of locomotion, fast limb movements, predatory movements, and a few other fast  
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8 138 responses in multicellular organisms. Only six species were tested for more than one response  
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10 139 type.

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12 140 For flicker fusion times  $T_F$ , we used the CFF data from Healy et al. (2013) (34 vertebrate  
13  
14 141 species) and Inger et al. (2014) (31 invertebrate species and 41 vertebrate species not considered  
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16 142 by Healy et al. 2013), plus 25 other CFF measurements. Our sample ( $T_F = 1/\text{CFF}$ , Table S2)  
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18 143 includes 130 measurements on 108 species. The values measured by behavioural ( $n = 26$ ) and  
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20 144 electroretinographic (ERG,  $n = 103$ , column M in Table S2) techniques are not significantly  
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22 145 different (Fig. S2C and Table S10); so, we pooled them together.

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25 146 The minimum times to move by one body length  $T_L$  were collected and analysed previously  
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27 147 from the measured maximum speeds  $V_{\max}$  of swimming and running organisms of length  $L$  as  $T_L$   
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29 148  $= L/V_{\max}$ ; this sample includes 458 measurements from 427 species (Table S3) and does not  
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31 149 include flying, whose maximum speed is not constrained by muscles (Meyer-Vernet and Rospars  
32  
33 150 2016).

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36  
37 151 For  $T_S$  and  $T_L$ , we distinguished unicellular and multicellular organisms and spermatozooids ( $T_L$   
38  
39 152 only), as specified in column U of Tables S1 and S3. For the three timescales, column Cla of  
40  
41 153 Tables S1-S3 defines groups of phylogenetically related species; they belong to the same class in  
42  
43 154 multicellular organisms and to the same kingdom according to the WoRMS database (World  
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45 155 Register of Marine Species, <http://www.marinespecies.org>) in unicellular organisms (except  
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47 156 spermatozooids). Further details on Tables S1-S3 are given in Supplementary material.

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51 157 Table S4 lists 14 mammalian species for which both minimum locomotor times  $T_L$  and  
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53 158 maximum mass specific metabolic rates (MSMR in W/kg) are known.

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## 160 2.2. *Body Mass*

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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  $M_{\text{kg}} = 11.2 L_{\text{m}}^{3.04}$  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  $T_{\text{F}}$  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.

## 174 2.3. *Temperature Effects*

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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,  $\exp(-E/k_{\text{B}}\theta)$ , where  $E$  is the  
180 activation energy of the process studied (in joules),  $k_{\text{B}}$ , the Boltzmann constant, and  $\theta$ , the  
181 temperature (in kelvins). Thus, the corrected time scale  $T_0$ , at the reference temperature  $\theta_0$ , of  
182 time  $T$  measured at temperature  $\theta$  is  $T_0 = T \exp(qE/k_{\text{B}})$ , 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

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3 184 range of species and traits (Dell et al. 2001). In the special case of  $T_S$ , we also applied a finer  
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5 185 standardization procedure distinguishing defence or movement away from a stimulus, like startle  
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8 186 responses, and consumption or movement toward a stimulus (almost all other responses), whose  
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10 187 mean activation energies are  $E = 0.4$  and  $0.7$  eV, respectively (Dell et al. 2001).

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#### 13 14 189 2.4. Statistical Analyses

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19 191 Statistics were computed on either data  $T$  or their log-transform ( $\log_{10} T$ ). In the main text, but not  
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21 192 in Supplementary material, all data ( $T$  and  $\log_{10} T$ ) were averaged per species, counting  
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23  
24 193 separately sperm cells (in  $T_L$  data, Table S3) and late developmental stages (for *Danio rerio* and  
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26 194 *Procambarus clarkii* in  $T_S$  data, Table S1). The data in each category ( $T_S$ ,  $T_F$  and  $T_L$ ) were  
27  
28 195 characterized by their medians and interquartile ranges IQR. Lognormal distributions were fitted  
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31 196 after determination of their parameters (mean  $\mu$  and standard deviation  $\sigma$ ) on log-transformed  
32  
33 197 data. However, for easier readability,  $\mu$  in log units was converted in seconds in text and figures  
34  
35 198 (except in Supplementary material Tables S7-S10), as  $\mu^* = 10^\mu$  ( $\mu^*$  is the geometric mean and  
36  
37 199 median of the lognormal distribution fitted to data  $T$ ). Similarly,  $\sigma$  was expressed as a  
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40 200 multiplicative standard deviation  $\sigma^* = 10^\sigma$  ( $\sigma^*$ , like  $\sigma$ , is dimensionless; it determines the  
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42 201 asymmetry of the distribution, and the interval  $[\mu^*/\sigma^*, \mu^*\sigma^*]$  covers a probability of 68.3 %, see  
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44 202 Limpert et al. 2001). The overall interval of variation in each timescale was expressed as the  
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47 203 percentiles 2.5 % and 97.5 %, which are less sensitive to outliers and sampling fluctuations than  
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49 204 the minimum and maximum; the ratio of these percentiles and its logarithm (denoted  $\delta T_{95}$ )  
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51 205 estimate the multiplicative range including 95 % of values. Statistical distributions were  
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54 206 compared with the Kolmogorov-Smirnov test. Least-square regressions of  $\log_{10} T_i$  against  
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56 207  $\log_{10} M$  and least-rectangle regressions of  $\log_{10} T_L$  against  $\log_{10} MSMR$  (Dagnelie 2011) were

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3 208 calculated and given as scaling equations  $T_i = T_0 M^\alpha$  in figures and their slope (also called scaling  
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5 209 exponent)  $\alpha$  as 95 % confidence intervals in the text. Tables S7-S10 provide details of ANOVA  
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7 210 and multiple comparisons of means using Tukey-Kramer adjustment method. We used the  
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10 211 significance level 5 % in all tests. We performed all statistics with the Matlab Statistical Toolbox  
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12 212 (The Mathworks, Natick, USA).

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17 214 3. EMPIRICAL RESULTS18  
19 21520  
21 216 3.1. *Statistical Distributions of Timescales and Comparisons*22  
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26 218 Simple response times,  $T_S$ , extend from 2.5 ms in the escape behaviour of the calanoid  
27  
28 219 copepod *Undinula vulgaris* to 485 ms in the acoustic response of the white whale *Delphinapterus*  
29  
30 220 *leucas*, with median 24 ms and IQR 43 ms. The distribution is lognormal (Fig. S1A), with  
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32 221 geometric mean  $\mu^* = 26$  ms and multiplicative standard deviation  $\sigma^* = 3.26$ . Critical fusion times  
33  
34 222  $T_F$  range from 2.5 ms in the black fire beetle *Melanophila acuminata* to 250 ms in the crustacean  
35  
36 223 isopod *Booralana tricarinata*, with median 24 ms and IQR 27 ms. The distribution is lognormal  
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38 224 (Fig. S1C) with  $\mu^* = 25$  ms and  $\sigma^* = 2.14$ . The times to move by one body length at maximum  
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40 225 speed  $T_L$  extend from 5 ms for a sea urchin to 2.8 s for a large spirochetes bacterium, with  
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42 226 median 71 ms and IQR 99 ms (Meyer-Vernet and Rospars 2016). The distribution is lognormal  
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44 227 with  $\mu^* = 78$  ms and  $\sigma^* = 2.73$  (Fig. S1B). Since most of the variability in the data comes from  
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46 228 the diversity of species, stimuli and measurement methods, such lognormal distributions are  
47  
48 229 expected if these factors act in a multiplicative way.

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50  
51 230 Figure 1 compares as boxplots the (log-transformed) timescales  $T_F$ ,  $T_S$  and  $T_L$ . Their relative  
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53 231 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*

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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  $5 \times 10^{-13}$  kg (green alga)  
240 and multicellular organisms from  $3 \times 10^{-9}$  (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  $4.7 \times 10^{-3}$  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  $\alpha$  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  $2 \times 10^{-6}$  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  $2.5 \times 10^{-3}$  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  $T_F = 0.026M^\alpha$  (Fig 3), with  $\alpha$  in the 95 % CI  $[-0.01, 0.06]$  (Table 2).

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3 256 The times to move by one body length at maximum speed  $T_L$  (Meyer-Vernet and Rospars  
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5 257 2016, Fig. 4) concern 426 species including microorganisms from  $10^{-16}$  kg (bacterium) to  
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7 258  $1.3 \times 10^{-8}$  kg (ciliate eukaryotic cell) and multicellular organisms from  $10^{-9}$  (copepod) to  $1.4 \times 10^5$   
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10 259 kg (blue whale). So,  $M$  varies by 21 orders of magnitude whereas 95 % of the  $T_L$  values lie  
11  
12 260 between  $21 \times 10^{-3}$  and 0.71 s. The times  $T_L$  in single cells ( $\mu^* = 145$  ms) are twice longer and  
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14 261 more variable than in multicellular organisms ( $\mu^* = 69$  ms), this difference being significant  
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16 262 (Table S8b, second line,  $p < 10^{-8}$ ). In both groups  $T_L$  increases slightly with mass, since the 95 %  
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18 263 CI of the slope of the regression line  $\alpha$  is [0.020, 0.14] for single cells and [0.028, 0.060] for  
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20 264 multicellular organisms (Table 2). However, the trend of the multicellular group results from the  
21  
22 265 largest vertebrates since for species under 50 kg the slope of the regression law  $\alpha$  is not  
23  
24 266 significantly different from zero (95 % CI is [-0.030, 0.11] (Table 2).  
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28 267 Since the maximum metabolic rate of organisms affects their maximum speed (Meyer-Vernet  
29  
30 268 and Rospars 2016), we studied also the dependence of  $T_L$  on maximum specific metabolic rates  
31  
32 269 (MSMR) in 14 species of mammals for which both values were determined (Table S5). The slope  
33  
34 270 of the regression lines of MSMR against body mass (Fig. S6A) and of  $T_L$  against MSMR (Fig.  
35  
36 271 S6B) are not significantly different from 0 and  $-1$  respectively, suggesting independence of  
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38 272 MSMR on mass and inverse dependence of  $T_L$  on MSMR.  
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## 43 274 4. DISCUSSION

44 275

### 45 276 4.1. *Variability and Mass Dependency of Timescales*

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47 278 Over the whole mass range, the variabilities of the timescales expressed by the ranges including  
48  
49 279 95 % of the data ( $\delta T_{95}$ , Table 1), are so small compared to the mass ranges ( $\delta M$ , Table 2), that  
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3 280 their ratios are always less than one in a million ( $10^{\delta T_{95}}/10^{\delta M}$ ). Indeed, 95 % of the simple  
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5 281 response times  $T_S$  (Fig. 2), of the visual resolution times ( $T_F = 1/\text{CFF}$ , Fig. 3) and of the minimum  
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7 282 locomotor times  $T_L$  (Fig. 4) lie within less than a factor of ten, five and six respectively of their  
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9 283 geometric mean, whereas the mass varies by 20, 8, and 21 orders of magnitude for  $T_S$ ,  $T_F$  and  $T_L$   
10  
11 284 respectively. This is noteworthy, given the diversity of sensorimotor systems and the huge mass  
12  
13 285 range, and suggests that these times are strongly constrained by physics, as was previously  
14  
15 286 proposed for  $T_L$ . The small variation of the visual resolution times is remarkable, given the  
16  
17 287 variation in spatiotemporal optical quality with eye size, which is correlated to body size (e.g.  
18  
19 288 Currea et al. 2018), and the large diversity of visual systems (e.g. Fernald 2000) and of strategies  
20  
21 289 of spatiotemporal summations. Although CFF is unrivaled to quantify the ability of an organism  
22  
23 290 to track a moving object, whether it is representative of other sensory systems is an open question  
24  
25 291 for further investigation. However, as suggested by a few reports (for example in olfaction,  
26  
27 292 Rumbo and Kaissling 1989, Lemon and Getz 1997, Smear et al. 2011, Jacob et al. 2017),  
28  
29 293 temporal resolution might reflect properties common to diverse neural networks rather than  
30  
31 294 specificities of the receptors (Butts et al. 2007, Panzeri et al. 2010) and, hence, be similar in the  
32  
33 295 visual and other sensory systems.

34  
35 296 Most of the overall variability results from variations at smaller mass ranges. Within uni- and  
36  
37 297 multi-cellular organisms considered separately, the mass-scaling exponents are not significantly  
38  
39 298 different from zero or result from a small-scale trend ( $T_L$  in large metazoans), so that the  $T_L$   
40  
41 299 (small) mass dependency in single cells appears as an exception that will need further data to be  
42  
43 300 interpreted. For  $T_S$  and  $T_L$ , differences between single cells and metazoans contribute to the  
44  
45 301 overall variability. The twice longer geometric mean of  $T_L$  in single cells (Table 1) is well  
46  
47 302 documented ( $n = 70$  species) but the six times longer one of  $T_S$  ( $n = 7$ ) should be confirmed on a  
48  
49 303 larger sample.

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3 304 Although outside the scope of this paper, we examined narrower mass ranges, i.e. groups of  
4  
5 305 related species of the same class (or kingdom in microorganisms) including more than three  
6  
7 306 species (Fig. S3, S4, S5 and Table S6). For most groups, the mass scaling exponents are positive  
8  
9  
10 307 with intercepts decreasing with mass, so that all the data still lie in a relatively narrow range, as  
11  
12 308 found previously for the mass specific metabolism (Makarieva et al. 2008, Hatton 2019) and its  
13  
14 309 maximum value (Makarieva et al. 2005). For simple response times  $T_s$ , the only exponent that  
15  
16 310 reaches statistical significance is that of mammals (Fig. S3) where the trend explains 42% of the  
17  
18 311 variance and agrees with previous studies (section 4.3). Although not significant, the trend in  
19  
20 312 bacteria stands out owing to the proportion of variance it explains (81 %) and its steep slope  
21  
22 313 ( $\alpha = 0.66$ ) which agrees with first-principle derivations (section 5). For the flicker fusion time, the  
23  
24 314 mass exponent of the small-scale regressions are not significantly different from zero. Finally, for  
25  
26 315 the minimum time to move by one body length, the positive mass scaling exponent of mammals  
27  
28 316 stems from large masses (the inflection point near 50 kg is apparent in Fig. 4), as noted and  
29  
30 317 interpreted by Meyer-Vernet and Rospars (2016); we shall return to this point in section 5.  
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#### 319 *4.2. Possible Errors Resulting from Biological, Methodological and Experimental Factors*

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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

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2  
3 326 small or no systematic variation with body mass in uni- and in multicellular organisms? Several  
4  
5 327 criticisms could be raised.

6  
7 328 First, one could object that the diversity of organisms, of sensory and motor mechanisms, and  
8  
9  
10 329 of experimental procedures hides any trend in the data. However, it is unlikely that the restriction  
11  
12 330 to more homogeneous data would reveal trends presently hidden because the smaller size of  
13  
14 331 samples would decrease the statistical significance. On the contrary, the diversity of species,  
15  
16 332 measurements and systems is indispensable to estimate reliably the variability and mean of the  
17  
18 333 timescales, independently of the specializations and limitations of taxa and systems. Our aim is to  
19  
20 334 transcend mass scalings holding within groups by considering large ranges of mass and  
21  
22 335 taxonomic groups.

23  
24  
25 336 Second, the evolution of different traits is correlated throughout a phylogenetic lineage so that  
26  
27 337 species values do not represent statistically independent data (Felsenstein 1985). This leads to  
28  
29 338 overestimation of degrees of freedom, which artificially narrows confidence intervals. Our major  
30  
31 339 finding that timescales lie within close bounds and that for unicellular (for  $T_s$ ) and multicellular  
32  
33 340 organisms (for all timescales) they do not significantly depend on mass would not be adversely  
34  
35 341 affected by any widening of confidence intervals (on the contrary for  $T_L$  in single cells) and is  
36  
37 342 therefore impervious to this criticism.

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39  
40 343 A third possible objection is that several experimental factors affecting the measurements have  
41  
42 344 not been considered explicitly. The electrical or behavioural measurement methods play a minor  
43  
44 345 role and correcting them would have practically no effect (Fig. S2 and Table S10 show that their  
45  
46 346 difference is not significant). However, the effect of temperature, which is an important  
47  
48 347 determinant of metabolism and behaviour, should be checked. We thus studied how correcting  
49  
50 348 the time scales of ectotherms to a standard temperature  $\theta_0 = 20$  °C would change our results (see  
51  
52 349 Methods). First, the temperature being unknown in several measurements, we considered the



1  
2  
3 350 worst-case scenario assuming that short time scales ( $T < \mu^*$ ) were measured at 10 °C, and would  
4  
5 351 thus be still shorter if they had been measured at  $\theta_0$ , and that long time scales ( $T \geq \mu^*$ ) were  
6  
7 352 measured at 30 °C, these two temperatures being close to the extremes in our data (Fig. S7A). For  
8  
9  
10 353 this preliminary test, we used the mean activation energy  $E = 0.66$  eV observed in a wide range  
11  
12 354 of species and traits (Dell et al. 2001), and studied how the percentage of timescales lying outside  
13  
14 355 the range  $[\mu^*/10, \mu^* \times 10]$  would be affected by temperature in this worst-case scenario. For all  
15  
16 356 timescales, this percentage is less than 3 % without standardization (Table S11a) and less than  
17  
18 357 10 % with standardization (Table S11b), except for  $T_s$  where it is 5 % and 22 % respectively.  
19  
20 358 Next, noting the greater sensitivity of  $T_s$ , we applied a finer standardization procedure to this  
21  
22 359 timescale, for which the temperature is known in 72 % of our data for ectothermic species, based  
23  
24 360 on the different mean activation energies of movements away from and toward a stimulus (see  
25  
26 361 Methods). This procedure leads to no significant change neither in the distribution of  $T_s$  values  
27  
28 362 (Fig. S7B) nor in the number of species beyond the limits (it remains the same, i. e. four, Fig.  
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30 363 S7). This indicates that our results in mean, variability and overall trend are robust with respect to  
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32 364 temperature.  
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#### 40 366 4.3. *Comparison with Previous Work*

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44 368 Several studies across a wide range of mass and life forms have found organisms' properties to  
45  
46 369 lie in a relatively narrow range, without mass scaling across groups, despite the size scaling  
47  
48 370 observed within groups. This is the case for the mass-specific metabolic rate (Makarieva et al.  
49  
50 371 2008, Hatton et al. 2019), its maximum value per unit of active mass (Makarieva et al. 2005), the  
51  
52 372 cross-section-specific forces exerted by muscles and molecular motors (Marden and Allen 2002,  
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2  
3 373 Marden 2005, Rospars and Meyer-Vernet 2016), and the minimum time to move by one body  
4  
5 374 length  $T_L = L/V_{\max}$  (McMahon and Bonner 1983, Meyer-Vernet and Rospars 2015, 2016).

7 375 However, for the simple response time  $T_S$  and the critical flicker fusion time  $T_F$ , previous  
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9  
10 376 studies concern only relatively small mass ranges and we have included these data. The mass  
11  
12 377 scaling of sensorimotor delays has been studied by More and Donelan (2018) in the particular  
13  
14 378 case of the stretch reflex – a monosynaptic reflex that governs the fastest neural response to  
15  
16  
17 379 peripheral stimuli in terrestrial mammals, with a determination of the different components and a  
18  
19 380 comparison with stance and stride durations. In our  $T_S$  sample, we have used the sum of these  
20  
21 381 components except the force generation delay (time between force onset and peak), in coherence  
22  
23 382 with the rest of our data, for which the response is measured by the onset of force production or  
24  
25 383 the onset of movement (which can begin before the production of peak force). These data points  
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27  
28 384 lie within the range of our general data set  $T_S$  for multicellular organisms, where the nerve  
29  
30 385 conduction delay is expected to be mainly responsible for the increase of  $T_S$  shown in figure 2 at  
31  
32 386 large mass. Indeed, the increase in nerve conduction speed due to increase in fibre diameter and  
33  
34 387 to myelination is too moderate to compensate for the increase in distance of conduction, because  
35  
36 388 of the trade-off between responsiveness and compactness (Castelfranco and Hartline 2016),  
37  
38 389 resolution (More et al. 2013), and energy cost (Perge et al. 2012). Let us compare the nerve  
39  
40 390 conduction delay estimated by More and Donelan (2018)  $T_{\text{cond}} = 5.3 M^{0.3}$  ms to the geometric  
41  
42 391 mean ( $T_S = 22$  ms) that we find for multicellular species (Table 1). This yields  
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44  
45 392  $T_{\text{cond}}/T_S = 0.24 M^{0.3}$ , which shows that the conduction delay becomes important only for large  $M$ ,  
46  
47 393 although even for the largest mammal studied (the elephant),  $T_S$  is only four times larger than its  
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49 394 average value.

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## 396 5. QUANTITATIVE INTERPRETATIONS FROM FIRST PRINCIPLES

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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).

### 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  $\eta \simeq 10^{-3} \text{ kg m}^{-1} \text{ s}^{-1}$ , a sphere of diameter  $d$  at  
415 temperature  $\theta$  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  $d \simeq 3 \text{ nm}$ , like the key signalling protein  
417 CheY (Bren and Eisenbach 2000), yielding a diffusion coefficient in water  $D \simeq 150 \text{ } \mu\text{m}^2/\text{s}$ .  
418 Assuming that the crowding of the cytoplasm decreases  $D$  by one order of magnitude (e.g. Dill et

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3 419 al. 2011, Mika and Poolman 2011) and that the sensor-to-motor distance equals the organism's  
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5 420 length  $L$ , we find the three-dimensional diffusion time  $L^2/6D$

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7  
8 421 
$$\tau_{\text{dif}} \approx 10 L_{\mu\text{m}}^2 \text{ ms.} \quad (1)$$
  
9

10 422 This timescale is the minimum response time  $T_s$  of a microorganism of size  $L$  if information is  
11  
12 423 transmitted through the cytoplasm by diffusion of signalling proteins, which is the most basic  
13  
14 424 process. With  $L \propto M^{1/3}$ , this would yield a mass variation  $T_s \propto M^{2/3}$ , as observed for bacteria (see  
15  
16 425 the leftmost regression line in Figure S3 with slope  $\alpha = 0.66$ , as given in Table S5). The median  
17  
18 426 mass of a bacterium of length  $L$  being  $M \simeq (3.3L)^3$  (Meyer-Vernet and Rospars 2016), the length  
19  
20 427 of a bacterium of mass  $10^{-15}$  kg ( $\mu_M^*$ , Table S6) is  $L \simeq 3 \mu\text{m}$ . We deduce from Eq. (1)  $T_s = 90$   
21  
22 428 ms, which agrees to better than a factor of two with the empirical value for bacteria ( $\mu^* = 144$  ms  
23  
24 429 in Table S5) and is close to the response time given by their regression line ( $T_s = 100$  ms for  
25  
26 430  $M = 10^{-15}$  kg, Table S6).

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31 431 Consider now multicellular organisms. For most of them, the responses are mediated by  
32  
33 432 conduction of information via electric pulses propagating through neurons, whose membrane  
34  
35 433 regulates the permeation of ions via an insulating lipid bilayer and proteins. The proteins act as  
36  
37 434 active ion channels and pumps and the lipid bilayer acts as a capacitance that enables charges to  
38  
39 435 accumulate and produce a potential across it. Biological membranes are also involved in sense  
40  
41 436 organs, via the concentration gradients they enable which produce active transport, whereas ion  
42  
43 437 channels play an essential role in signal transduction (Martinac and Cox 2016). The role of ions  
44  
45 438 to alter charge and thus protein conformation is essential in signal transduction in both uni- and  
46  
47 439 multicellular organisms (Clapham 2007). For example, paramecia use  $\text{Ca}^{2+}$  ions and show  
48  
49 440 dynamic changes in the electrical properties of their membrane in response to stimuli, as do  
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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  $\epsilon_m$ , so that the capacitance is

$$447 \quad C \simeq \epsilon_0 \epsilon_m S/a, \quad (2)$$

448 where  $\epsilon_0$  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  $\epsilon_0 \epsilon_m S U^2/a$ , which agrees with values  
450 in the literature (Aiello 2000). Using two biological properties common to living matter: the mass  
451 density  $\rho \simeq 10^3 \text{ kg/m}^3$  and the maximum metabolic rate per unit mass of active tissue  
452  $b_M \simeq 2 \times 10^3 \text{ W/kg}$  (Makarieva et al. 2005), the maximum power available to this surface  $S$  of  
453 membrane of mass  $\rho a S$  is

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

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  $e = 1.6 \times 10^{-19} \text{ C}$  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

$$459 \quad T_S \simeq \epsilon_0 \epsilon_m W_0^2 / (\rho b_M e^2 a^2) \quad (4)$$

460 Substituting the typical dielectric constant of lipids  $\epsilon_m \simeq 2$ , a membrane width  $a \simeq 6 \text{ nm}$  – 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)

$$463 \quad W_0 \simeq e^2 / (4\pi \epsilon_0 a) \quad (5)$$

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2  
3 464 we obtain  $T_S \simeq 14$  ms, close to the empirical mean simple response time  $T_S$  of metazoans (22  
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5 465 ms).

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10 467 *5.2. Flicker Fusion Time*

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15 469 Let us now estimate the timescale  $T_F$ , assuming that it is limited by the membrane time constant

16  
17 470  $\tau_m$ . For a surface  $S$  of membrane of width  $a$  and resistivity  $r_m$ , the electrical resistance is

18  
19 471  $R = r_m a/S$  and the capacitance is given by (2), so that the time constant  $\tau_m = RC$  is given by

20  
21  
22 472 
$$\tau_m = r_m \varepsilon_0 \varepsilon_m. \quad (6)$$

23  
24 473 To estimate a basic value for the resistivity  $r_m$ , independent on the details of the system, we

25  
26 474 consider again energy constraints. In an electrical circuit of resistance  $R$ , submitted to the

27  
28 475 potential difference  $U$ , the power is  $U^2/R$ . Using the maximum power available (3), we deduce

29  
30 476 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

31  
32 477 of magnitude  $U \simeq W_0/e$ , we deduce  $\tau_m$ , which yields the flicker fusion time  $T_F \simeq \tau_m$  (reflecting the

33  
34 478 ability of the membrane to resolve a time-varying signal)

35  
36  
37  
38 479 
$$T_F \simeq \varepsilon_0 \varepsilon_m W_0^2 / (\rho b_M e^2 a^2) \simeq T_S \simeq 14 \text{ ms} \quad (7)$$

39  
40 480 close to the empirical value of  $T_F$  (25 ms), and in agreement with our empirical result  $T_F \simeq T_S$ .

41  
42 481 The absence of significant increase of  $T_F$  for the largest masses (Fig. 3), contrary to what is

43  
44 482 observed for  $T_S$  (Fig. 2) suggests that the signal conduction time and hence the organism length  $L$

45  
46 483 plays a minor role in  $T_F$ , contrary to  $T_S$ .

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52 485 *5.3. Minimum Locomotion Time*

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1  
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3 487 An order of magnitude estimate of the minimum time to move by one body length  $T_L = L/V_{\max}$   
4  
5 488 was derived by Meyer-Vernet and Rospars (2016) from the invariance over the whole domain of  
6  
7 489 life of the force per cross-sectional area exerted by molecular motors and muscles ( $f \simeq W_0/a^3 \simeq$   
8  
9 490  $2 \times 10^5 \text{ N/m}^2$ , Rospars and Meyer-Vernet 2016), and the two basic quantities considered above,  
10  
11 491 mass density  $\rho$  and mass-specific (per unit mass of active tissue) metabolic rate at maximum  
12  
13 492 activity  $b_M$ . The maximum speed was estimated as  $V_{\max} \simeq L \rho b_M / f$  for swimming and running  
14  
15 493 organisms (including microorganisms) of length  $L$  satisfying  $L \lesssim (f/\rho)^{3/2}/b_M \simeq 1.4 \text{ m}$  –  
16  
17 494 corresponding roughly to  $M \simeq 50 \text{ kg}$  (Meyer-Vernet and Rospars 2016). This yields  $T_L \simeq L/V_{\max}$ ,  
18  
19 495 the minimum time to move by  $L$

$$20 \quad T_L \simeq f / (\rho b_M) \simeq W_0 / (\rho b_M a^3) \simeq 100 \text{ ms} \quad (8)$$

21  
22 496 for  $M \lesssim 50 \text{ kg}$ , which agrees to better than a factor of two with the empirical value (59 ms,  
23  
24 497 geometric mean of  $T_L$  for all organisms of mass  $M < 50 \text{ kg}$ , Table 1). The increase in  $T_L$  observed  
25  
26 498 for larger organisms (Fig. 4) has been interpreted by dynamic constraints, yielding  
27  
28 499

$$29 \quad T_L \simeq L (\rho/f)^{1/2} \quad (9)$$

30  
31 500 (Meyer-Vernet and Rospars 2016), in agreement with the known maximum speed of about 15  
32  
33 501 m/s (e.g. McMahon and Bonner 1983, Garland, 1983, Iriarte-Diaz 2002).

34  
35 502 It is interesting to note that our estimates of the minimum times for response (4), for vision  
36  
37 503 (7), and for moving by one body length (8) all yield timescales proportional to the inverse of the  
38  
39 504 maximum mass-specific metabolic rate (per unit of active mass). This suggests that, since the  
40  
41 505 metabolic rate varies with mass within groups of related species, these time scales may depend  
42  
43 506 not only on body mass within groups of related species but also on metabolic rates. This is shown  
44  
45 507 for  $T_L$  in mammals (Fig. S6B), which is inversely proportional to the maximum mass-specific  
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2  
3 509 metabolic rate, as expected from (8) if the proportion of active tissue in the body mass does not  
4  
5 510 vary in the range considered in the regression.  
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7

8 511 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  
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10 512 magnitude, to be compared to the empirical ratio  $T_L/T_S = 78/26 = 3$ , suggesting that fast reacting  
11  
12 513 species are also fast moving.  
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## 17 515 6. CONCLUSIONS

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21 517 We have shown that across the whole of mobile life, from bacteria to large vertebrates, the simple  
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23 518 response time  $T_S$  lies in a relatively narrow range, with 95 % of species reacting in a time that  
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25 519 differs by less than one order of magnitude from the mean, in striking contrast to the 20 orders of  
26  
27 520 magnitude difference in body mass. The simple response time does not display significant scaling  
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29 521 with body mass across groups in unicellular organisms nor in multicellular ones, although it is  
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31 522 almost six times larger in the former life form. The absence of large-scale trend does not preclude  
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33 523 – and is indeed compatible with various scalings valid in narrower ranges of size and taxa, as is  
34  
35 524 known for the specific metabolic rate. However, within narrow ranges, the detailed characteristics  
36  
37 525 of the organisms must be considered and it is only on larger scales that these variations can be  
38  
39 526 transcended.  
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44 527 This simple response time  $T_S$  is close to a well-studied sensory timescale (the inverse of the  
45  
46 528 critical flicker fusion frequency for vision)  $T_F$ , and is a few times smaller than the minimum time  
47  
48 529 to move by one body length  $T_L$ , with all time scales lying in a relatively narrow range. Since this  
49  
50 530 narrow range suggests that these time scales may be strongly constrained by physics and basic  
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52 531 properties of life, independently of the structure or mass of the organism, we have performed  
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2  
3 532 tentative simple estimates of  $T_S$  and  $T_F$  based on fundamental physicochemical constants and  
4  
5 533 basic properties common to motile organisms.  
6

7  
8 534 It is fair to note that the agreement between these simple estimates of minimum time scales  
9  
10 535 (for sensing, for reacting and for moving) and the measurements is only indicative of the  
11  
12 536 dominant constraints in play (e.g. Phillips and Milo 2009), since several mechanisms may be  
13  
14 537 operating in parallel. For example, one tenth of second is in the middle of the range of protein  
15  
16 538 folding time scales, which however spans six orders of magnitude (e.g. Lane and Pande 2013)  
17  
18 539 and close to the maximal turn-over rate of the most abundant enzyme in the biosphere (e.g.  
19  
20 540 Flamholz et al. 2019). The relation  $T_S \approx T_F < T_L$  found from the data (Fig. 1) and tentatively  
21  
22 541 interpreted from first-principles, is reminiscent of symmorphosis (Weibel et al. 1991) and  
23  
24 542 expected to be favoured by evolution since it is indicative of an optimum state. Indeed, if  $T_S < T_F$   
25  
26 543 the sensory resolution would be in excess over motor control whereas if  $T_S > T_F$  the response  
27  
28 544 would be limited by sensory performance, so that in both cases, at least one component of the  
29  
30 545 nervous system would be out of tune and wasting energy or space (Laughlin 2001). Likewise, the  
31  
32 546 evolution is expected to favour organisms for which the sensory and response organs act fast  
33  
34 547 enough with respect to their moving performances. It is noteworthy that since the first-principle  
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36 548 estimate (8) of  $T_L$  holds for both uni- and multi-cellular organisms (Meyer-Vernet and Rospars  
37  
38 549 2016), the estimate (1) of the minimal response time  $T_S$  yields a maximal length  $L$  of a few  
39  
40 550 micrometres in order to ensure  $T_S \leq T_L$  when the response is mediated by diffusion, as observed  
41  
42 551 for bacteria  
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49 552 These preliminary results encourage further research on the response times of mobile  
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51 553 organisms and their fundamental bases. They might also possibly be used to infer properties of  
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53 554 extinct species since the reconstructed speed (e.g. Hutchinson and Garcia 2002) and size (e.g.  
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3 555 Hutchinson et al. 2011) of the giant dinosaur *Tyrannosaurus rex* yield a time to move by one  
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5 556 body length  $T_L \approx 1$  s for a mass  $M \approx 10^4$  kg, which is close to the value expected from (9) and  
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7 557 would put *Tyrannosaurus rex* in the middle of the data of extant animals of this size in figure 4.  
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3 559 *Ethical Statement*  
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5 560 The present article is based on a meta-analysis. No live animals were used.  
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10 562 *Data Accessibility*  
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12 563 The datasets supporting the article are included in the Supplementary Material.  
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17 565 *Competing Interests*  
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19 566 We have no competing interests.  
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24 568 *Author's Contributions*  
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26 569 J.-P.R. and N.M.-V. each made significant and substantial contributions to this study in terms of  
27

28 570 the conception, design, data collection and interpretation of results, as well as preparing the  
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30 571 manuscript. J.-P.R. contributed primarily to the statistical analyses and N.M.-V. to the physical  
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32 572 analyses.  
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734 TABLE 1. Summary statistics of timescales (in ms) for unicellular, multicellular and all species

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736 Timescale	<i>n</i>	min	max	$Q_{2.5}$	$Q_{97.5}$	$r_{95}$	$\delta T_{95}$	med	IQR	$\mu^*$	$s^*$	out <sub>95</sub>	out <sub>10</sub>
737 -----													
738 $T_S$ all	81	2.5	485	4.7	311	66	1.82	24	43	26	3.26	4	4
739 $T_S$ unicell	7	18.0	350	18.0	350	19	1.29	200	195	129	3.17	0	0
740 $T_S$ multicell	74	2.5	485	4.7	238	51	1.71	23	35	22	2.93	4	3
741 $T_S$ multic<50kg	68	2.5	240	4.6	148	32	1.51	18	28	19	2.64	4	1
742 -----													
743 $T_F$ all multic	106	2.5	250	4.2	100	24	1.37	24	27	25	2.14	5	1
744 -----													
745 $T_L$ all	427	5.3	2778	20.9	706	34	1.53	71	99	78	2.73	22	11
746 $T_L$ unicell	70	5.3	2778	11.9	2778	234	2.37	123	213	145	3.86	2	9
747 $T_L$ multicell	357	12.5	2525	22.3	567	25	1.41	61	82	69	2.40	18	3
748 $T_L$ multic<50kg	300	12.5	657	21.5	408	19	1.28	50	61	59	2.22	14	3
749 -----													

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;  $\mu^*$ , geometric mean (ms);  $s^*$ , multiplicative standard deviation; out<sub>95</sub>, number  
 755 of values outside [ $Q_{2.5}$ ,  $Q_{97.5}$ ]; out<sub>10</sub>, 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 -----

759		<i>n</i>	$\log_{10}T_0$	$\alpha$	IC <sub>1</sub>	IC <sub>2</sub>	$\mu_M^*$	$\delta M$	$r_\alpha$	$\delta T_\alpha$	$r^2$	<i>P</i>	Sig
760													
761	$T_S$ all	81	-1.69	-0.033	-0.06	-0.01	-3.10	19.59	0.2	-0.64	7	0.02	1
762	$T_S$ unicell	7	-0.35	0.038	-0.41	0.49	-14.17	3.70	1.4	0.14	1	0.83	0
763	$T_S$ multicell	74	-1.58	0.036	-0.01	0.08	-2.05	12.11	2.7	0.44	3	0.12	0
764	$T_S$ multic<50kg	68	-1.77	-0.024	-0.08	0.03	-2.45	9.89	0.6	-0.24	1	0.36	0
765													
766	$T_F$ all multic	106	-1.57	0.023	-0.01	0.06	-1.93	8.25	1.6	0.19	2	0.19	0
767													
768	$T_L$ all	427	-1.13	-0.010	-0.02	-0.00	-2.86	21.05	0.6	-0.20	1	0.03	1
769	$T_L$ unicell	70	0.10	0.078	0.02	0.14	-12.01	8.01	4.2	0.63	10	0.01	1
770	$T_L$ multice	357	-1.11	0.044	0.03	0.06	-1.06	14.15	4.2	0.62	7	0.00	1
771	$T_L$ multic<50kg	300	-1.25	-0.010	-0.03	0.01	-1.72	10.70	0.8	-0.10	0	0.34	0
772													

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 +  $\alpha \log_{10} M$ ;  $\alpha$ , allometric coefficient; [IC<sub>1</sub>, IC<sub>2</sub>], 95% confidence intervals of slope  $\alpha$ ;  $\mu_M^*$ , mean

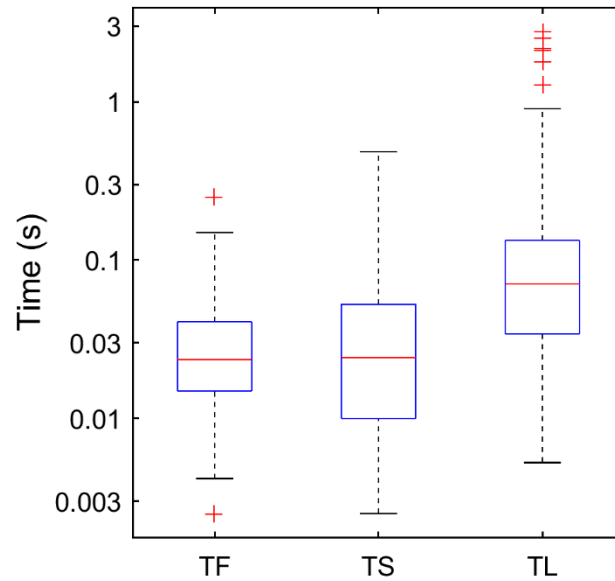
776  $\log_{10} M$ ;  $\delta M$ , mass range of the category,  $\delta M = \log_{10}(M_{\max}/M_{\min})$ , with  $M_{\max}$  and  $M_{\min}$  masses of

777 heaviest and lightest species in the category;  $r_\alpha$ , 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

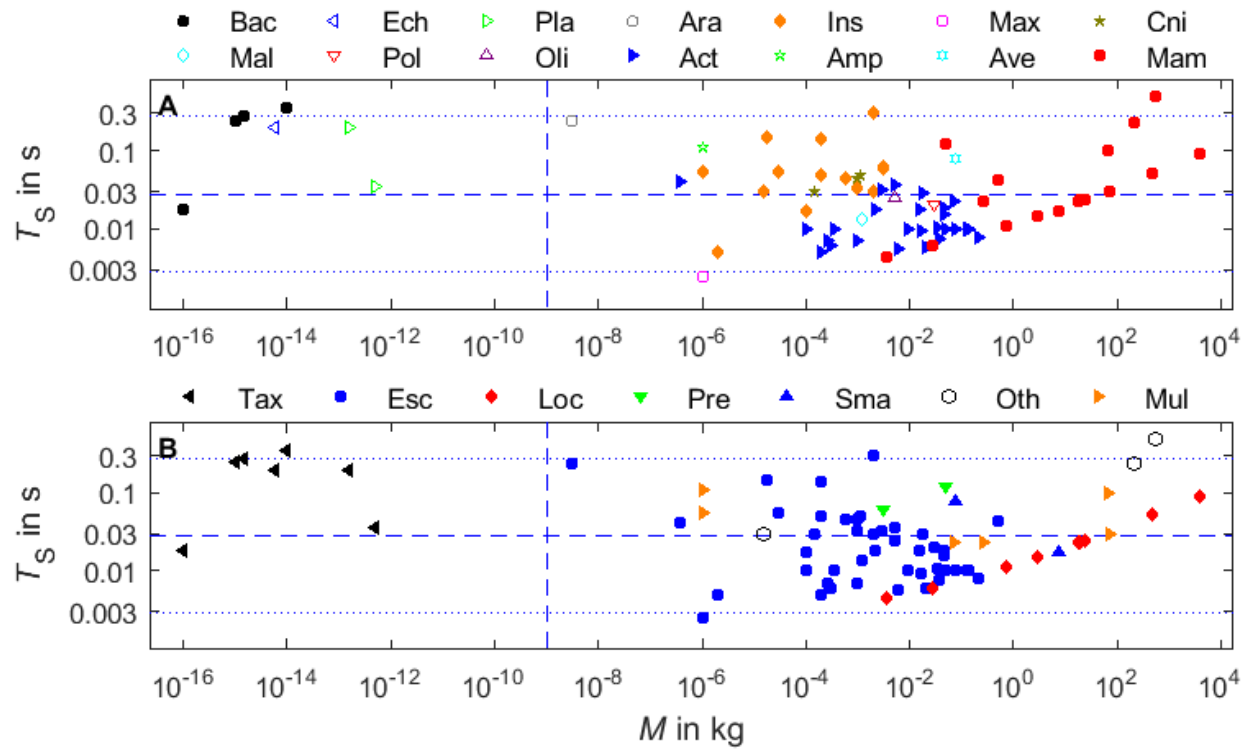
779 slope  $\alpha = 0$ ; Sig, slope  $\alpha$  of regression line significantly different from zero (1) or not (0).

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  $1.5 \times \text{IQR}$ . Outliers (red crosses) are values beyond the end  
 786 of the upper whiskers. ANOVA and multiple comparisons of means (Supplementary material,  
 787 Table S7):  $T_F = T_S \neq T_L$ .

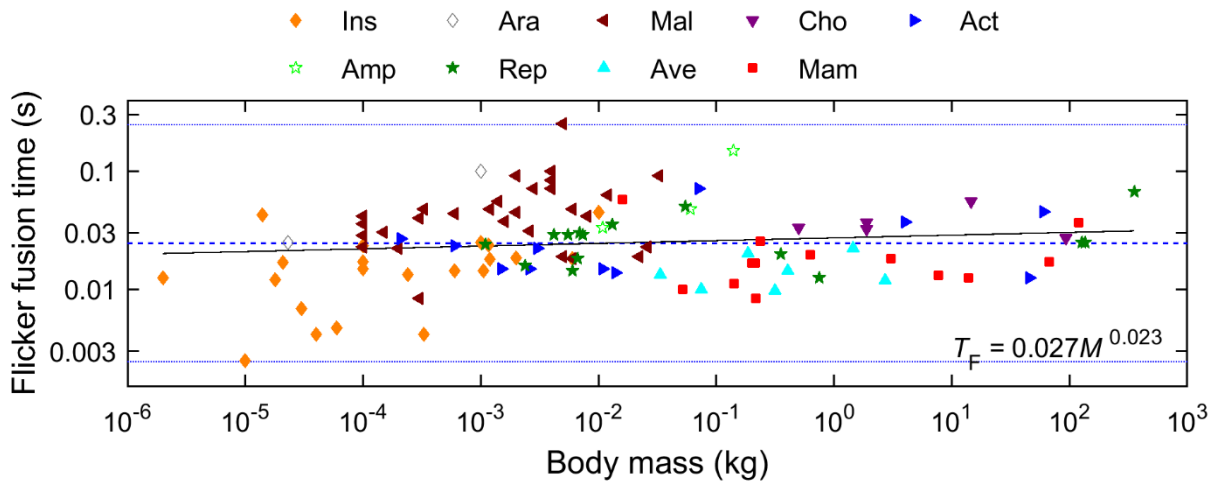
788



789  
790 **Figure 2.** Simple response times  $T_S$  versus cell or body mass  $M$  ( $n = 81$ ). For clarity, the scale on  
791 the y-axis is 1.5 times larger than on the x-axis .

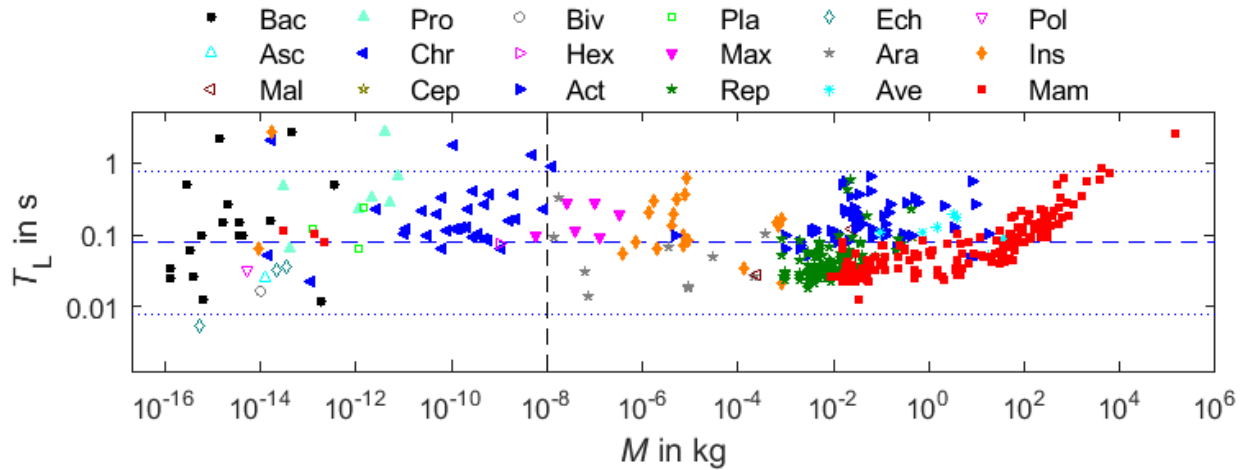
792 **A.** Taxonomic groups. Groups with three species or less shown as empty symbols, other groups  
793 as filled symbols. Bacteria (Bac,  $n = 4$ ), Echinodermata (Ech, 1, sperm), Planta (Pla, 2),  
794 Arachnida (Ara, 1), Insecta (Ins, 16), Hexanauplia (Hex, 1; copepods), Cnidaria (Cni, 3),  
795 Malacostraca (Mal, 2; crustaceans), Polychaeta (Pol, 1; bristle annelids), Oligochaeta (Oli, 1;  
796 earthworms), Actinopterygii (Act, 28; cartilaginous fishes), Amphibia (Amp, 1), Aves (Ave, 1;  
797 birds), Mammalia (Mam, 18). The horizontal dashed line is the geometric mean  $\mu^*$  (26 ms) with  
798 values larger and smaller by one order of magnitude dotted. Vertical dashed line separates  
799 unicellular from multicellular organisms. Intermediate-scale regression laws for, from left to  
800 right, single cells (solid black line), multicellular organisms above 50 kg excluded (dashed black  
801 line) and included (solid black line). Slopes not significantly different from zero.

802 **B.** Types of response. Species tested for a single type of response shown in filled symbols: cell  
803 chemotaxis and phototaxis (Tax,  $n = 7$ ), startle with escape (Esc, 46), sensory control of  
804 locomotion (Loc, 11), predatory movement (Pre, 6), small movement in startle of birds and  
805 mammals (Sma, 2), other behaviour (Oth, 3; see Table S1). Species tested for two or more types  
806 of response (empty symbol, Mul, 6). Dashed and dotted horizontal lines as in A.



807  
 808 **Figure 3.** Flicker fusion times  $T_F$  versus body mass  $M$  ( $n = 106$ ) according to taxonomic groups,  
 809 shown as colour of empty and filled symbols as in Fig. 2. Arachnida (Ara,  $n = 2$ ), Insecta (Ins,  
 810 21), Malacostraca (Mal, 29; crustaceans), Cho (Chondrichthyes, 5; cartilaginous fishes),  
 811 Actinopterygii (Act, 11; ray-finned fishes), Amphibia (Amp, 3), Reptilia (Rep, 15), Aves (Ave, 7;  
 812 birds), Mammalia (Mam, 13). The horizontal dashed line is the geometric mean  $\mu^*$  (25 ms) with  
 813 values larger and smaller by one order of magnitude dotted. Scaling regression law in inset. Slope  
 814 not significantly different from zero.

815



816  
 817 **Figure 4.** Times to move by one body length at maximum speed  $T_L$  versus cell or body mass  
 818 ( $n = 426$ ) according to taxonomic groups. For clarity, the scale on the y-axis is 1.5 times larger  
 819 than on the x-axis. Groups with three species or less shown as empty symbols, other groups as  
 820 filled symbols. Bacteria (Bac,  $n = 17$ ), Protozoa (Pro, 7; flagellates), Bivalvia (Biv, 1, sperm),  
 821 Planta (Pla, 3), Echinodermata (Ech, 3, sperm), Polychaeta (Pol, 1, sperm; bristle annelids),  
 822 Ascidiacea (Asc, 1, sperm; sea squirts), Chromista (Chr, 32; ciliates), Hexanauplia (Hex, 6;  
 823 copepods), Arachnida (Ara, 10), Insecta (Ins, 20; 2 sperm), Malacostraca (Mal, 3; crustaceans),  
 824 Cephalopoda (Cep, 1), Actinopterygii (Act, 55; cartilaginous fishes), Reptilia (Rep, 96), Aves  
 825 (Ave, 9; birds), Mammalia (Mam, 161; 3 sperm). The horizontal dashed line is the geometric  
 826 mean  $\mu^*$  (78 ms) with values larger and smaller by one order of magnitude dotted. Vertical  
 827 dashed line approximately separates unicellular and multicellular organisms. Intermediate-scale  
 828 regression laws in inset as in Fig. 2. Slopes significantly different from zero, except for  
 829 multicellular organisms under 50 kg.