

Does Critical Flicker-Fusion Frequency Track the Subjective Experience of Time?

Jason Schukraft

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Executive Summary

The subjective experience of time is a morally significant aspect of well-being. Critical flicker-fusion frequency (CFF) has occasionally been suggested as a proxy for the subjective experience of time. CFF, a measure of visual temporal resolution, is the threshold at which a rapidly flickering light appears to glow steadily. CFF thresholds have been measured in more than 70 different species across 30+ orders and 3 phyla. Values range from ~7 Hz to ~200 Hz. Putatively similar animals sometimes possess very different CFF thresholds.

If differences in CFF thresholds correlate with differences in the subjective experience of time, they probably only do so for species that characteristically inhabit relatively bright environments, rely heavily on vision to learn about the world, and exhibit high behavioral plasticity. CFF may be correlated with the subjective experience of time, but it does not causally govern the subjective experience of time.

In general, natural selection should favor animals with better temporal resolution if (1) there are fitness-relevant fast-moving objects or quickly-unfolding events in the local environment and (2)the animals can take fitness-improving actions as a result of the greater temporal resolution. When the fitness-improving actions are likely to require conscious decision-making, we can expect that increases in temporal resolution to generally be accompanied by increases in the rate of subjective experience. However, limited experimental evidence suggests that CFF doesn't track differences in duration estimates that are plausibly a consequence of differences in the subjective experience of time. Moreover, it's possible to provide an evolutionary explanation for differences in CFF that doesn't appeal to differences in the subjective experience of time.

Itentatively estimate there is a ~40% chance that CFF values rough-

Introduction and Context

This post is the fourth in Rethink Priorities' moral weight series. The primary goal of the series is to improve the way resources are allocated within the effective animal advocacy movement. A secondary goal is to improve the allocation of resources between human-focused cause areas and nonhuman-animal-focused cause areas. In the first post I lay the conceptual framework for the rest of the series, outlining different theories of welfare and moral status and the relationship between the two. In the second post I present and evaluate two methodological schema for measuring and comparing capacity for welfare and moral status. In the third post I explain what the subjective experience of time is, why it matters, and why it's plausible that there are morally significant differences in the subjective experience of time across species. In this, the fourth entry in the series, I explore critical flicker-fusion frequency as a potential proxy for the subjective experience of time. In the fifth, sixth, and seventh entries in the series, I investigate variation in the characteristic range of intensity of valenced experience across species.

The Importance of Finding a Proxy for the Subjective Experience of Time

Physiological and neurological differences across different types of animals may give rise to characteristically different temporal experience. The subjective experience of time refers to the felt duration of events. It's possible that for a given duration of objective time, some animals experience subjectively longer durations than other animals. Animals with a faster rate of subjective experience are capable of experiencing more subjective moments per objective unit of time than animals with a slower rate of subjective experience. As a rough analogy, one can imagine that animals with faster than human rates of subjective experience perceive the ly track the subjective experience of time under ideal conditions. world as if it were a movie played in what a human would describe



are capable of experiencing more subjective moments per objective unit of time than animals with a slower rate of subjective experience. As a rough analogy, one can imagine that animals with faster than human rates of subjective experience perceive the world as if it were a movie played in what a human would describe as slow-motion, while animals with slower than human rates of subjective experience perceive the world as if it were a movie played in what a human would describe as fast-forward.¹) All else equal, for a stimulus of the same subjective negative intensity, animals with a faster rate of subjective experience will suffer more than animals with a slower rate of subjective experience. (Similarly, positive stimuli will produce more pleasure. In a previous post, I estimated there is a ~70% chance that there exist characteristic differences in the subjective experience of time across species.

One's rate of subjective experience affects a fundamental aspect of one's experiences. All plausible theories of welfare accept that one's experiences are a major determinant of one's well-being. Thus, despite our moral uncertainty, we can say with confidence that the subjective experience of time is a morally significant topic.

Given this importance, it's worth thinking carefully about how to detect differences in the subjective experience of time. Such differences are probably not amenable to direct measurement; after all, the subjective experience of time is *subjective*. Nonetheless, there may be certain empirically measurable proxies that, under the right conditions, at least roughly track differences in the subjective experience of time. Below, I explore critical flicker-fusion frequency (CFF), a measure of visual temporal resolution, as one such proxy.

CFF is a useful metric to explore for two reasons. First, there is a plausible—though hardly airtight—connection between temporal resolution (defined below) and the subjective experience of time. Second, there already exists a wealth of cross-species data on CFF thresholds. By my count scientists have determined CFF thresholds for at least 70 species across more than 30 orders and 3 phyla. Although the exact methods for probing CFF vary, the values themselves appear to be directly comparable across species. Since CFF values are cardinal numbers, we can make claims like 'yellowfin tuna have a CFF that is twice as high as loggerhead sea turtles.' CFF values thus potentially give us a way to quantify and compare the subjective experience of time. For these reasons,

CFF is a useful case study in attempting to measure a morally significant component of experience.

On the other hand, I want to make plain that at this time it would be unwise to unreflectively incorporate CFF values into cost-effectiveness estimates as a way to gauge the comparative moral value of different animals. Even if CFF does track the subjective experience of time, there is no guarantee that a relative difference in CFF values between two animals represents a proportional difference in the rates of subjective experience for those animals. There could be (possibly non-linear) scale invariance. And although it seems as if CFF values are comparable across animals, interspecies differences may make such comparisons less informative than they appear. In general, the greater the morphological, ecological, and phylogenetic distance between animals, the more wary we ought to be about comparing their CFF values.²

It would probably be naive to assume that there exists a single metric that adequately tracks the subjective experience of time. To learn about differences in the subjective experience of time, we ought to examine a wide variety of independent potential proxies. When those proxies all or mostly point in the same direction, we can be more confident in the conclusions we draw. Critical flicker-fusion frequency is plausibly a decent place to start that investigation.

Critical Flicker-Fusion Frequency

Imagine a light source alternating between on and off. Now imagine the rate of alteration slowly increasing. At some point, if the light flickers quickly enough, an observer will no longer perceive the flickering and the light will appear to glow steadily.³ Critical flicker-fusion frequency (CFF) is "the threshold at which an animal ceases to perceive a flickering light source as a series of flashes, but rather as a continuous stream of light" (Inger et al. 2014: 2). This threshold characteristically varies across species (and, to a milder extent, across individuals of the same species).

CFF measures an animal's visual temporal resolution. Temporal resolution is the rate at which a perceptual system samples information about its environment. Temporal resolution is analogous to the refresh rate of a monitor. The higher a perceptual system's

³ This (relatively poor quality) <u>Youtube video</u> demonstrates the phenomenon.



¹ However, it's important to remember that this is only a metaphor. Visual perception is importantly disanalogous to mechanical recording devices. As <u>Hol-combe 2009</u> notes, "Video cameras have a single temporal limit set by the frame rate. The human visual system has multiple temporal limits set by its various constituent mechanisms" (216).

² As an extreme example, note that relatively simple machines can process visual information and thus be assigned CFF thresholds. But in the absence of other behavioral cues, we probably shouldn't think such inorganic systems are conscious. The fact that some simple robot has a higher CFF threshold than some human doesn't tell us that the robot has faster subjective experiences than the human if we think the robot doesn't have subjective experiences at all.

refresh rate, the faster it absorbs new information, resulting in a more fine-grained temporal perception of the world. Greater temporal resolution means higher temporal precision, generally enabling an animal to better track fast-moving objects in its vicinity or respond more quickly to rapidly unfolding events.

CFF is an indicator of visual information intake. Given eyes of the same spatial resolution, animals with higher CFF thresholds can absorb more visual information per unit of time than animals with lower CFF thresholds (Jura 2019: 2).⁴ CFF is measured as a frequency and expressed in hertz (Hz). "CFF is a measure of a visual system's ability to resolve rapid stimulus change, and is defined as the maximum temporal frequency at which a light can flicker before being perceived as continuous" (Umeton, Read, & Rowe 2017: 2). The speed at which a light needs to flicker before it is perceived as continuous depends on a number of factors, including the light's wavelength, the light's intensity, the background lighting conditions, the subject's body temperature, and the subject's retinal position. CFF values generally specify "the highest threshold value found in any condition, representative for a particular species" (<u>Jura 2019</u>: 2). In the literature, maximum CFF is sometimes indicated as 'CFF $_{\rm max}$ ' or 'mCFF.' In what follows, I'll leave the qualifier 'maximum' implicit unless it is necessary to make a point.

CFF values are determined using behavioral or electroretinogram (ERG) procedures (Inger et al. 2014: 2).⁵ "In behavioural studies, CFF is measured through conditional training with the subject trained to respond to a change in its perception of a light flashing. For example, Lisney et al. (2011) conducted behavioural tests in domestic chickens, *Gallus gallus*, through choice experiments using flickering and nonflickering stimulus windows with choice of the correct stimulus rewarded with food. This is repeated over a range of light intensities and flicker frequencies until individuals can no longer distinguish between the stimuli. In ERG studies, a direct measurement of the electrical response of the retina in reaction to a flashing light source is used as a measure of CFF" (<u>Healey et al. 2013</u>: 686).⁶ In what follows, I generally won't distinguish between the two measurement procedures. However, the

two procedures do not always deliver the same result: the behavioral method often produces lower values (Inger et al. 2014: 2). Moreover, there may be theoretical reasons to prefer the behavioral procedure. The ERG procedure reveals the mechanical limits of the visual system. The mechanical limits of the visual system set an upper bound on a CFF threshold, but there is no a priori guarantee that the *perceived* threshold matches the upper bound (though there is good reason to think they are correlated). In contrast, the behavioral procedure directly reveals the threshold at which there is a subjective perceptual switch from a flickering to a steadily glowing light. Since we are concerned here with the connection between CFF and the subjective experience of time, it may be more appropriate to focus on the procedure that depends on subjective perceptual experience.⁷

If CFF is a good approximation for time perception, then lower CFF values represent slower rates of subjective experience and higher CFF values represent faster rates of subjective experience. That is, animals with higher CFF thresholds experience more subjective moments per objective unit of time than animals with lower CFF thresholds. To return to the analogy above, the higher an animal's CFF, the more the world resembles a movie played in slow-motion, and the lower an animal's CFF, the more the world resembles a movie in fast-forward. Seeing the world with greater temporal resolution generally allows an animal to consciously track fast-moving objects with more precision. (See Figure 1.)



Figure 1: Difference between the actual movement of a ground squirrel [CFF = 120 Hz] (box a), the movement as perceived by a conspecific (box b), and the movement as perceived by a short-eared owl [CFF = 70 Hz] (box c) (source: Healy et al. 2013: $686)^8$

4 "It [CFF] is used as a measure of temporal resolution of visual information processing, representing a maximum number of bits of information that can be detected in a unit time. Higher CFF values correspond to higher resolutions, as more information is absorbed over a temporal window of the same length and more rapid changes in a stimulus can be detected, as opposed to lower CFF values, when information is integrated over longer time windows" (Jura 2019: 2).

8 This figure is slightly misleading because it averages motion trajectory without incorporating motion blur. The owl does not perceive the squirrel as smoothly



^{5 &}quot;CFF values are determined either by using electroretinography (ERG) to measure the electrophysiological response of the retina to flickering light of various frequencies, or by examining the spontaneous or taught behavioural response to flickering light. Using either method the CFF is taken as the frequency at which the subject ceases to respond to an increase in flicker frequency" (Inger et al. 2014: 2).

⁶ See Eisen-Enosh et al. 2017 for a detailed technical evaluation of CFF measurement methods.

⁷ On the other hand, CFF values are supposed to represent the maximum value at which the perceptual switch occurs. As noted above, for any particular measurement, this threshold is influenced by a variety of environmental conditions. Since it is difficult to fully control for all variables that influence CFF, the ERG procedure might better reflect the true maximum.

Some Caveats

All metrics that measure complicated phenomena are subject to some amount of random noise and most measures are biased under some conditions. The question at hand is not whether critical flicker-fusion frequency perfectly reflects the subjective experience of time. Surely it does not. The relevant question is whether differences in CFF values ever correlate with differences in the subjective experience of time and, if they do, to what extent and under what conditions.

If CFF does track the subjective experience of time, it probably only does so for a subset of animals. It's important to remember that CFF is a visual measure. As such, it is inevitably biased against creatures that inhabit low-light environments, like nocturnal or benthic animals⁹ (Inger et al. 2014: 2).¹⁰ It is also biased against creatures that primarily rely on non-visual senses, like hearing (e.g., bats), smelling (e.g., guinea pigs), and whisking (e.g., rats). The lower CFF thresholds for these animals probably do not give us evidence that their rates of subjective experience are correspondingly lower. Whatever evolutionary advantage a faster rate of subjective experience confers, it seems like that advantage would generally accrue across sensory modalities, rather than being restricted to vision. (For instance, all else equal, echo-locating bats with better temporal resolution would be better predators than conspecifics with worse temporal resolution.) The existence of fast-moving, highly maneuverable nocturnal animals give us plausible reason to think that differences in the subjective experience of time won't be wholly captured by visual measures such as CFF.

The question is also not whether the mechanisms responsible for CFF thresholds are the exact same mechanisms that govern the subjective experience of time. CFF might be correlated with the subjective experience of time but not causally responsible for the subjective experience of time. Characteristic differences in CFF might be manifestations of characteristic differences in the subjective experience of time even if there are some factors that influence CFF but not the subjective experience of time and some factors that influence the subjective experience of time but not CFF. What we want to know is whether differences in CFF thresholds provide evidence for differences in rates of subjective experience." If they do, we want to know how strong the evidence is.

As noted above, CFF thresholds are measured as maximum values.¹² At any given moment, one's actual CFF threshold depends on a variety of environmental factors. We know that actual CFF thresholds don't track the subjective experience of time because actual CFF thresholds are more malleable than our subjective experience of time. For instance, we know changes in lighting conditions alter an individual's actual CFF thresholds. (Dimmer environments produce lower values.¹³) However, it's clear from experience that one's subjective rate of experience doesn't slow down in the dark. This fact shows us that the mechanisms that govern CFF are not the exact same mechanisms that govern the subjective experience of time. However, the neural mechanisms that govern the subjective experience of time might shape and constrain the range of values that an individual's CFF threshold can take. Maximum CFF thresholds may thus tell us something about the upper limit of an animal's subjective experience of time. When one enters a dark room, one's actual CFF threshold declines, but one's maximum CFF threshold does not decline.

The degree to which CFF values give us evidence about the subjective experience of time may also depend on the behavioral plasticity of the animal in question. As I explain below, the case that CFF values track the subjective experience of time rests in part on the idea that, under the right conditions, animals with subjectively longer moments in which to make conscious decisions accrue a fitness advantage over conspecifics with subjectively shorter moments.¹⁴ But for animals with comparatively rigid behavioral repertoires, there may be fewer instances in which conscious decision-making is important. If most of an animal's behaviors are hard-wired, then increased conscious deliberation time doesn't confer as much of a fitness advantage. Higher temporal resolution (as measured by CFF) could still benefit these an-

moving along the averaged trajectory. Instead, the owl perceives blurred motion centered on the troughs and peaks of the averaged trajectory. Thanks to Gavin Taylor for this point.

9 Benthic animals are animals that occupy the lowest level of a body of water. In deep waters, the benthic zone receives little sunlight.

10 "It has been known for some time that animals adapted for low light environments tend to have lower CFFs than animals found in more intense light environments" (Inger et al. 2014: 2).

11 We also want to know if differences in the subjective experience of time characteristically induce differences in CFF thresholds.

12 What counts as a *maximum* value is sometimes contentious. As noted above, different measurement techniques produce slightly different values (e.g., behavioral procedures tend to produce lower values than ERG procedures).

13 This is true across species. For the bonnethead shark, <u>McComb et al. 2010</u> report scotopic (dim light) CFF at 25.6 Hz and photopic (bright light) CFF at 31 Hz. For mice, <u>DeRamus & Kraft 2018</u> report scotopic (dim light) CFF at 18.4 Hz and photopic (bright light) CFF at 44.4 Hz.

14 For instance, ground squirrels with subjectively faster rates of experience will have more (subjective) time to decide what to do about an approaching hawk than conspecifics with slower rates of subjective experience and thus will tend to make better decisions, thereby surviving to reproductive age at greater rates



imals by, say, more quickly triggering instinctive reflexes, but such reflexes might operate outside conscious experience.¹⁵

As an illustration of the importance of behavioral plasticity, consider two species with extremely good visual temporal resolution: golden-mantled ground squirrels and tsetse flies.¹⁶ Ground squirrels appear to exhibit a significant degree of behavioral plasticity. To warn conspecifics of danger, they emit a variety of different alarm calls depending on the location and type of predator.¹⁷ When it spots a threat, a ground squirrel must ascertain whether or not it has been seen, the probability that it can return to the burrow without being captured, and whether and what type of alarm call to sound. With so many options available to it, it seems ground squirrels are well-placed to benefit from subjectively increased time for conscious decision-making. In contrast, the behavior of tsetse flies is probably more rigid. If tsetse fly behavior is largely hardwired, they would not benefit from subjectively increased time for conscious decision-making (though they probably benefit from increased CFF in other ways). Thus, their high CFF may not be indicative of a correspondingly fast rate of subjective experience.

These caveats aside, I think CFF is as good a place as any (and better than most) to start a discussion about measuring differences in the subjective experience of time. Even if we come to believe that CFF is not itself an especially good metric for the subjective experience of time, reflecting on the reasons why CFF might and might not track the subjective experience of time could teach us valuable lessons about how to identify better metrics in the future. There are also broader lessons to be learned. CFF introduces a metric of moral significance that gives an ordinal ranking of animals that differs from our intuitive estimates. As such, it provides a reminder that intuitive estimates of comparative moral value may be influenced by unjustified speciesist prejudices. At the very least, considering CFF prompts us to appreciate our deep uncertainty about the way we value animals.

Reasons to Think CFF Tracks the Subjective Experience of Time

Section Summary

Under some conditions, differences in temporal resolution (as measured by CFF) might be correlated with differences in the

subjective experience of time. Increasing temporal resolution has energetic costs. In general, natural selection should favor animals with better temporal resolution if (1) there are fitness-relevant fast-moving objects or quickly-unfolding events in its environment and (2) the animal can take fitness-improving actions as a result of the greater temporal resolution. When the fitness-improving actions are likely to require conscious decision-making, we can expect that increases in temporal resolution will generally be accompanied by increases in the rate of subjective experience.

Details

The idea that critical flicker-fusion frequency is correlated with characteristic differences in the subjective experience of time across species appears to be taken seriously in the scientific community. Here is one example: <u>Boström et al. 2016</u> is a study of critical flicker-fusion frequency in three species of birds, including the European pied flycatcher, a type of insectivorous songbird with extremely good visual temporal resolution. The paper includes a <u>supplemental video</u> of two *Calliphora vomitoria* flies. In the video, the same recording of the flies is presented twice: once at 40 frames a second, described in the video as "*Calliphora vomitoria* as seen by the human eye," and again in slow motion, described in the video as "*Calliphora vomitoria* at 40% speed, as seen by the flycatcher." (See Figure 2.) The inclusion of this video implicitly suggests that the authors believe the flycatcher has a faster rate of subjective experience than humans.



Figure 2: The flight paths of two blue bottle flies sampled from high-speed video at the rate of the visual system of a human (A) and at the rate of a pied flycatcher (B) (source: <u>Boström et al. 2016</u>: 4)

The relationship between CFF and the subjective experience of time is also sometimes made explicit. Bartosz Jura of the <u>Nalecz</u> <u>Institute of Biocybernetics and Biomedical Engineering</u> has explored the connection. He writes, "As the values of CFF display

16 About 2 and 2.4 times higher than humans, respectively.

17 Some of the alarm calls are ultrasonic and inaudible to predators (Wilson & Hare 2004).



¹⁵ If an animal's degree of behavioral plasticity influences the degree to which we think CFF reflects subjective experience, then this is an example of a *combination effect*: "A property might raise the moral status of one being but not another, because it might raise moral status only when combined with certain other properties" (Harman 2003: 177-178). I discuss combination effects in the <u>first</u> and <u>second</u> posts in this series.

a specific species-varied pattern that can be attributed to evolutionary-ecological processes, suggesting that the persistence of visual percepts is precisely tuned in particular species, it seems reasonable to assume that the persistence of other types of contents of conscious experience will also be shaped evolutionarily, in accord with the visual system's CFF, so that they last as long as it is suitable for individuals from species living in given circumstances, not too long and not too short, likely being proportional to intervals separating behaviorally relevant events in which a corresponding type of information is processed" (Jura 2020: 3).¹⁸ Jura concludes, "Subjective time flows with variable rate, as we know it from introspection, and it seems that it flows with yet different rates for individuals from different species" (Jura 2020: 6).

It's helpful to unpack this argument in some detail. The first premise is that CFF thresholds are shaped by evolutionary and ecological pressures. This claim is well-founded. Animals have temporal resolutions that are adapted to the environments they inhabit. For example, CFF values are generally correlated negatively with body mass and positively with metabolic rate, at least in vertebrates (<u>Healey et al. 2013</u>: 689).¹⁹ These correlations have a tidy evolutionary explanation. Harvesting and processing temporal information is costly; investing in increased temporal resolution is only beneficial if the increased resolution is useful. High temporal resolution is only useful if an animal can react quickly to the faster pace of information coming in. For physical reasons, smaller animals are generally able to react more quickly than larger animals (<u>Healey et al. 2013</u>: 689).²⁰ A faster metabolism also aids maneuverability and reaction time (<u>Healey et al. 2013</u>:

686).²¹ So small animals with fast metabolisms are better poised to utilize fine-grained temporal information. When these animals are prey to fast-moving predators or are predators to fast-moving prey, increased temporal resolution appears especially beneficial (Healey et al. 2013: 685-686).²²

However, nothing in the above paragraph necessitates that increased temporal resolution must influence *conscious* experience. The quick reactions that allow animals with high temporal resolution to evade predators or capture prey might occur outside conscious experience. We know that visual information can activate alerting and orienting attentional networks in the absence of conscious awareness (Lu et al. 2012). To reach the conclusion that CFF tracks differences in the subjective experience of time, we need an additional premise. Jura suggests that "the persistence of other types of contents of conscious experience will also be shaped evolutionarily, in accord with the visual system's CFF, so that they last as long as it is suitable for individuals from species living in given circumstances."

The basic idea is that brains that take in fast-paced visual stimuli probably have to operate faster in order to keep up. Brains that operate faster are plausibly capable of faster rates of subjective experience. If the fast-paced visual stimuli that is coming in is consciously processed, then other conscious processes probably run at a similar rate. Thus, animals with better temporal resolution will tend to have faster subjective experiences.²⁵ Valtteri Arstila, a philosopher with specialty in the neuroscience and psychology of time, suggests "we have experiences of time slowing down because improvements in temporal resolution mirror the overall

18 Jura adds that he thinks this argument only holds for animals that predominantly rely on vision and for which we have independent reason to think are conscious (personal correspondence).

19 "Our results show that, while there is considerable variability in the ability to resolve temporally dynamic visual information across vertebrates, body mass and metabolic rate act as important general constraints on this ability" (Healey et al. 2013: 689).

20 "manoeuvrability, a vital component of an individual's ability to respond to the environment, may be one of the main factors determining whether it is necessary to invest in costly temporal information processing. Manoeuvrability, as defined by the ability to change body position or orientation, generally scales negatively with body mass. [...] owing to the laws of physics, larger animals physically respond less quickly to a stimulus. Hence we expect selection against costly investment in sensory systems with unnecessarily high temporal resolution in large animals, as information on such timescales can no longer be utilized effectively" (<u>Healey et al. 2013</u>: 689).

21 "Two intrinsic factors that may shape the costs and benefits of the temporal resolution of the sensory system, in particular with respect to their effects on an individual's ability to interact with the environment on short timescales, are body size and metabolic rate. As larger body sizes decrease manoeuvrability (Heglund and Taylor, 1988, Dudley, 2002, Biewener, 2003, Sato et al., 2007, Vogel, 2008, Hedrick, 2011, Watanabe et al., 2012) and higher metabolic rates increase both manoeuvrability and the physiological ability to process information (Laughlin, 2001, Franz and Ronacher, 2002), we hypothesized that smaller organisms and those with higher metabolic rates perceive temporal change on finer timescales" (Healey et al. 2013: 686).

22 "The ability to integrate information over fine timescales, that is, at high temporal resolution, is thus fundamental to many aspects of an organism's ecology and behaviour. [...] From an evolutionary perspective, a trade-off exists between the demand for information at high temporal resolution and the costs of its acquisition given the energetic demands associated with increased rates of neural processing in the visual system (Laughlin 2001). This trade-off is likely to be shaped by various ecological (e.g. mode of predation) and environmental factors (e.g. light levels) as well as intrinsic factors (e.g. morphology) that will ultimately shape an organism's optimal temporal resolution for sensory perception. For example, predators of slow-moving prey may require less temporal resolution than predators that engage in active pursuit of fast-moving prey, such as raptors catching prey during flight" (<u>Healey et al. 2013</u>: 685-686).

23 Brian Tomasik has expressed <u>a similar view</u>: "Smaller animals, in general, have greater temporal resolution of vision in the sense that they can tell that a light source is flickering up to a higher frequency than bigger animals can. This suggests the possibility that smaller animals might, in general, have higher rates of 'subjective experience,' loosely defined."



enhancement in neural processing, not only in the mechanisms of visual perception. Temporal resolution improvement understood in this way makes more sense: not only would our sensory systems provide us with more information but we would also be able to grasp this new information because our attention and other processes would be speeded up as well" (Arstila 2012: 5). To see if differences in CFF reflect broader differences in temporal processing, it's helpful to look at non-visual temporal judgments.

There is preliminary evidence that differences in temporal perception are roughly correlated across sensory modalities, at least in some animals (including humans). A temporal order threshold is defined as the shortest time interval between two stimuli necessary for a person to identify the correct temporal order. Fink et al. 2006 reports that "temporal-order thresholds have been assessed over different sensory modalities, and results have shown approximately the same values for auditory, visual and tactile stimulation" (344). Ten years later, the psychologist Marc Wittmann reports the same: "The more precise a person's temporal perception is, the smaller the interval between the stimuli can be-and the lower the temporal order threshold. Determining this temporal threshold of perception leads to similar results, irrespective of the senses and kinds of stimuli involved" (Wittman 2016: 25). Thus, for animals that utilize multiple senses, we might expect high CFF values to imply increased temporal resolution across sensory modalities.

To my knowledge, there has not been a large-scale, systematic study to determine the level of correlation of comparative temporal resolution in different senses across species.²⁴ In the absence of such a review, we can only draw tentative conclusions. For example, songbirds have excellent visual and auditory temporal resolution. And visual and olfactory temporal resolution appear to be correlated in some crustaceans and insects (low resolution in both cases for crustaceans, high resolution in both cases for insects).²⁵ More data and more data analysis would be required to confirm these potential correlations and to find others.

If characteristic differences in CFF reflect characteristic differences in the experience of time, it is probably because characteristic differences in CFF reflect characteristic differences in temporal processing. This is independently plausible, as noted above. We know that an individual's actual CFF threshold depends on environmental conditions in a way that the subjective experience of time does not. So if CFF is correlated with the subjective experience of time, it is only the *maximum* CFF thresholds (that is, the highest thresholds under ideal conditions) that are correlated with the subjective experience of time. If maximum but not actual CFF thresholds are correlated with the subjective experience of time, it must be the case that there is some neurological mechanism that governs the subjective experience of time that also influences maximum CFF.²⁶

The question remains, however, whether differences in temporal processing, even if they are generalized across sensory domains, reflect differences in conscious experience. Unfortunately, the mechanisms of temporal processing are poorly understood, and so we can as yet only conjecture how general changes in temporal processing affect conscious experience.²⁷ Moreover, differences in temporal processing might not affect conscious experience in the same way for different animals. One complication already noted is that the evolutionary advantage of faster subjective experience might depend on the behavioral plasticity of the animal in question. Deeper investigation will probably uncover other complications.

Reasons to Think CFF *Doesn't* Track the Subjective Experience of Time

Section Summary

Limited experimental evidence suggests that CFF doesn't track differences in duration estimates that are plausibly a consequence of differences in the subjective experience of time. It's possible to provide an evolutionary explanation for differences in CFF

24 Of course, the comparisons will only be informative if the compared animals regularly utilize the senses for which temporal resolution is being compared. Echo-locating bats might have excellent auditory temporal resolution but terrible visual temporal resolution. That sort of discrepancy wouldn't provide (much) evidence against the view that temporal resolution tracks the subjective experience of time—merely a reminder that *if* te mporal resolution tracks the subjective experience of time, it only does so under certain conditions.

25 See the <u>third post</u> in this series for more details.

26 The relationship between the two might be causal: whatever neural mechanism governs the subjective experience of time might also put an upper limit on CFF. But it might also be the case that the two features (rate of subjective experience and CFF) are selected for in tandem even in the absence of a causal connection. The ability to consciously perceive time faster is presumably costly, so natural selection might only select for that ability in animals that happen to have high temporal resolution (as measured by CFF). The more information an animal consciously processes, the more helpful it is to have more time to consciously deliberate about what to do with that information. Conversely, increased temporal resolution (as measured by CFF) isn't particularly helpful if the animal can't act on the information revealed by the increased resolution. Since faster subjective experience gives an animal more (subjective) time to incorporate information into the decision-making process, it seems like creatures with high temporal resolution would benefit from a faster rate of subjective experience. In short, higher CFF thresholds make faster rates of subjective experience more useful and vice versa.

27 See <u>Appendix 2</u> in the third post in this series for more details on theories of temporal representation in the brain.



7

that doesn't appeal to differences in the subjective experience of time. Given the complex nature of temporal processing, it seems unlikely that differences in the subjective experience would correlate well with a relatively simple metric like CFF.

Details

One way CFF might fail to track differences in the subjective experience of time is if there are no differences in the subjective experience of time across species.²⁸ In what follows, however, I will set that possibility aside. The question in this section is *conditional on the existence of significant differences in the subjective experience of time, why might CFF fail to track those differences*? Even allowing that differences in the subjective experience of time exist, there are still many obstacles on the inferential path from differences in CFF to differences in the subjective experience of time.

As above, I won't here be concerned with whether differences in CFF *perfectly* track differences in the subjective experience of time. We know that is not the case. Animals that inhabit low-light environments tend to have lower CFF thresholds because they rely less on visual perception. For these animals, other sensory measures of temporal resolution may provide better evidence for differences in the subjective experience of time.²⁹ In what follows, I'll restrict my concern to animals that inhabit brightly lit environments and utilize visual perception to navigate those environments.

There are two means by which the correlation between CFF and the subjective experience of time could break down: (1) differences in CFF could fail to reflect differences in the subjective experience of time, and (2) differences in the subjective experience of time could fail to be reflected in differences in CFF. I'll take these two possibilities in turn.

CFF is a measure of the temporal resolution of a visual system. Better temporal resolution allows an animal to track movement better. But it's not the case that one's ability to track movement necessarily corresponds to differences in the subjective experience of time. Imagine yourself in a brightly-lit room, trying your best to track the movement of a fly in flight. Now imagine that you dim

the lights in the room such that you can't track the movement of the fly with the same precision as you could with the room brightly lit. The fly doesn't appear faster in the dim room.³⁰ Or, if there's a sense in which the fly *does* appear faster, this appearance doesn't extend to the whole of one's temporal experience. The pitch of the fly's buzzing doesn't change, for instance.

So differences in the ability to track movement do not by themselves generate differences in the subjective experience of time. But characteristic differences in the ability to track movement might still be *correlated* with characteristic differences in the subjective experience of time, especially across species. Differences in CFF appear to be the product of differential evolutionary pressures.³¹ The ability to track movement better only confers a fitness advantage if that ability benefits the animal in some way. For example, predators that track movement better might be able to capture prey more easily. Prey that track movement better might be able to evade capture more easily. So for our purposes, the question is *can differences in the ability to track movement confer a fitness advantage large enough to explain differences in CFF without concomitant differences in the rate of subjective experience?*

It seems to me there is a plausible case that the answer to this question is 'yes.' Increases in temporal resolution (as measured by increases in CFF) may enable faster reaction without any accompanying increase in the rate of subjective experience. Much of the sensory information that animals (including humans) absorb is processed unconsciously. Differences in the speed of unconscious reactions don't reveal anything about subjective experience. Many impressively quick actions in the animal kingdom are probably the product of fixed action patterns. The flight stabilization mechanisms that allow hummingbirds to flit from flower to flower in the blink of an eye probably operate below conscious awareness.³² In flies, tracking and pursuit initiation mechanisms are triggered by fairly simple rules and appear to be hardwired.³³ These animals may benefit from fine temporal resolution even without a concomitant increase in the subjective experience of time. As an analogy, consider that humans benefit from spinal cord reflexes that operate more quickly than conscious experience. If one's

28 See the <u>third post</u> in this series for a discussion of the general case for the existence of characteristic differences in the subjective experience of time across species.

29 See the <u>third post</u> in this series for discussion of non-visual measures of temporal resolution.

³² See <u>Ros & Biewener 2016</u> and <u>Ibbotson 2017</u> for more on hummingbird flight stabilization. Humans also have a sensory-motor system that governs balance, and this system operates below our conscious awareness. (People don't typically realize how many microadjustments one's body continually makes to successfully carry a load of laundry up a flight of stairs without falling over.) In birds, flight stabilization mechanisms are governed by a homologous brain region. 33 See <u>Maimon, Straw, & Dickinson 2008</u> for an overview of simple decision-making algorithms in fruit flies.



³⁰ It seems to me the best description of the phenomenological difference between the two cases is that the fly appears *blurrier* in the dim room compared to the bright room.

³¹ This appears to be a widespread assumption in the literature, but it seems possible that differences in CFF are merely the accidental byproduct of differences in some other feature that has been subject to evolutionary pressure.

hand brushes against a hot stove, the hand is immediately pulled back, faster than the conscious sensation of pain is produced and much faster than one could consciously decide to remove the hand.

So it seems we could plausibly explain differences in temporal resolution (as measured by CFF) without positing differences in the subjective experience of time. There is also evidence that differences in the subjective experience of time aren't always captured by differences in CFF.³⁴

According to at least two studies, changes in duration estimates aren't accompanied by concomitant changes in CFF. David Eagleman and his collaborators have studied the relationship between systematic differences in temporal resolution and temporal perception. In one study, Eagleman and Vani Pariyadath exposed subjects to the classic oddball illusion: "in a repeated presentation of auditory or visual stimuli, an unexpected object of equivalent duration appears to last longer" (Pariyadath & Eagleman 2007: 1). (See Figure 3.) When the oddball image was displayed, Eagleman and Pariyadath checked to see whether other measures of temporal perception changed. They found that no such change occurred: "We here show that when a sound or visual flicker is presented in conjunction with an unexpected visual stimulus, neither the pitch of the sound nor the frequency of the flicker is affected by the apparent duration dilation. This demonstrates that subjective time in general is not slowed; instead, duration judgments can be manipulated with no concurrent impact on other temporal judgments" (Pariyadath & Eagleman 2007: 1).



Figure 3: The Oddball Illusion (source: Pariyadath & Eagleman 2007: 2)

For our purposes, a natural response to this experiment is to contend that the oddball illusion is just that: an *illusion*. Our temporal *judgments* can be manipulated in a variety of interesting ways, but differences in temporal judgments need not be the product of differences in temporal *experience*. (See <u>Appendix 1</u> in the third post in this series for an elaboration of this position.) However, a second experiment more directly bears on the relationship between duration estimates and the subjective experience of time.

It's commonly reported that during frightening events, such as automobile accidents or combat in warfare, time seems to slow down.³⁵ Eagleman, along with Chess Stetson and Matthew Fiesta, sought to experimentally test this claim. To do so, the trio first measured the CFF thresholds of subjects under normal conditions. Next, they measured the CFF of subjects as they fell 31 meters through the air in controlled free fall at the Zero Gravity amusement park in Dallas, Texas. (See Figure 4.) Such an experience is probably as close to a time-altering frightening event as researchers can ethically induce in their subjects. Consistent with reports of time dilation during frightening experience, individual subjects reported their own fall appeared to last on average 36% longer than the time that they estimated elapsed during the falls of fellow subjects. However, the CFF of the subjects did not show any corresponding improvement.³⁶ If frightening events do induce changes in the subjective experience of time and a 31 meter free fall is frightening in this respect, it appears that CFF does not capture this change.

³⁶ "Observers commonly report that time seems to have moved in slow motion during a life-threatening event. It is unknown whether this is a function of increased time resolution during the event, or instead an illusion of remembering an emotionally salient event. Using a hand-held device to measure speed of visual perception, participants experienced free fall for 31 m before landing safely in a net. We found no evidence of increased temporal resolution, in apparent conflict with the fact that participants retrospectively estimated their own fall to last 36% longer than others' falls. The duration dilation during a frightening event, and the lack of concomitant increase in temporal resolution, indicate that subjective time is not a single entity that speeds or slows, but instead is composed of separable subcomponents. Our findings suggest that time-slowing is a function of recollection, not perception: a richer encoding of memory may cause a salient event to appear, retrospectively, as though it lasted longer" (Stetson, Fiesta, & Eagleman 2007: 1).



³⁴ It might be thought that a faster rate of subjective experience would necessarily entail an improvement in CFF. After all, if the world were slowed down like a movie in slow-motion, then it would be easier to distinguish temporally close flashes of light. However, it's helpful to remember that the movie-in-slow-motion metaphor is only applicable if all forms of temporal processing are slowed or accelerated in tandem. As <u>Holcombe 2009</u> notes, "Video cameras have a single temporal limit set by the frame rate. The human visual system has multiple temporal limits set by its various constituent mechanisms" (216). Differences in the subjective experience of time (understood as the number of subjective moments one undergoes in a given objective duration) might manifest as differences in high-level visual processing without affecting lower-level visual mechanisms.

^{35 &}quot;Car crash victims, pilots forced to eject from their planes, rock climbers suffering serious falls, and other survivors of life-threatening danger, reliably report that the traumatic events which they experienced appeared to last much longer than events of the same objective length in normal conditions" (Phillips 2013: 228). See footnote 4 in Phillips 2013 for citations to support this claim.



Figure 4: Subjects fell 31 meters from the apex of the tower and were asked to identify a pair of digits randomly generated by the rapidly alternating LED lights (source: <u>Stetson, Fiesta, & Eagleman 2007</u>: 2)

Of course, there are many ways to challenge this experiment.³⁷ Although a 31 meter free fall is a novel experience, the participants knew what they were getting into and knew that the fall was completely safe. So perhaps we should not expect a difference in the subjective experience of time in this sort of scenario.³⁸ And even if there were differences in the subjective experience of time, the small sample size (n=20) and complex experimental setup could make such differences hard to detect. For this reason, it would be interesting to see this sort of experiment replicated, perhaps with first time skydivers or bungee jumpers.³⁹

Moreover, other experimental evidence paints a somewhat different picture. <u>Hagura et al. 2012</u> describe "a novel type of time distortion that occurs during the motor preparatory period before execution of a ballistic reaching movement. Visual stimuli presented during this period were perceived to be prolonged, relative to a control condition without reaching, and their flicker rate was perceived as slower. Moreover, the speed of visual information processing became faster, resulting in a higher detection rate of rapidly presented letters. These findings indicate that the visual processing during motor preparation is accelerated, with direct effects on perception of time" (Hagura et al. 2012: 4404). The researchers conclude that because "the time dilation, slowing down of perceived flicker frequency and the increase in letter-detection rate all occurs at the same action preparatory period, we believe that these effects are related to each other" (Hagura et al. 2012: 4405). More experiments of this type could potentially shed light on the relationship between CFF and the subjective experience of time.⁴⁰

A final consideration against the view that CFF tracks the subjective experience of time is that by all accounts, temporal processing is incredibly complex. There does not appear to be a single, unitary mechanism for processing or representing time (Jura 2019: 1). Different brain regions appear to be responsible for the temporal processing of different modalities and time intervals (Matthews & Meck 2014: 429). Thus, there does not appear to be a unitary mechanism that governs the subjective experience of time that could easily co-vary with an ostensibly unrelated measure like CFF. Of course, this complexity doesn't *rule out* the possibility that an animal's maximum CFF co-varies with its characteristic rate of subjective experience. It does, however, make this possibility somewhat less likely.

Current Credences

Based on the probabilities expressed below, my current overall credence that critical flicker-fusion frequency roughly tracks the subjective experience of time under ideal conditions is **0.39** (90% subjective confidence interval: 0.33 to 0.45).⁴¹

(1) Humans sometimes experience genuine differences in the subjective experience of time: **0.45**

(2) Conditional on the truth of (1), there are characteristic differences in the subjective experience of time across species: **0.9**

37 See Arstila 2012 (especially pp. 3-5) for general criticism of the conclusions that the researchers drew from the experiment.

41 See this Guesstimate model for the math.



³⁸ Of course, if there were no differences in the subjective experience of time, the difference in duration estimates becomes a bit harder (though by no means impossible) to explain.

³⁹ One problem with the Stetson, Fiesta, & Eagleman study is that they did not actually *ask* the subjects if time seemed to slow down during their jumps. Instead, Stetson, Fiesta, & Eagleman merely present circumstantial evidence in the form of differences in duration estimates. But we know that duration estimates are vulnerable to a number of biases. So the first step in replicating the Stetson, Fiesta, & Eagleman study should be to interview skydivers and bungee jumpers to see what percentage (if any) remember the feeling as of time slowing down during their first jump. If they don't report any time dilation, we would need to identify different activities that can be safely replicated in which participants report time slowing down.

⁴⁰ A complementary approach would be to investigate subjects with certain types of brain damage. Marc Wittman reports that "on average aphasic patients with brain damage need longer intervals of time between stimuli in order to recognize sequence. This fact might indicate the existence of an inner rhythm that has been decelerated. That said, on the whole patients do not report that the world around them is passing too quickly" (Wittman 2016: 32). However, there do appear to be *some* (albeit rare) clinical reports of accelerated time experience. See, for instance, <u>Binofski & Block 1996</u>.

(3) Conditional on the falsity of (1), there are characteristic differences in the subjective experience of time across species: **0.55**

(4) There are characteristic differences in the subjective experience of time across species: **0.71**

(5) Conditional on the truth of (4), CFF correlates with the subjective experience of time under all conditions: **0.01**

(6) Conditional on the truth of (4), CFF correlates with the subjective experience of time under ideal conditions:42 **0.55**

CFF Values Across Species

In what follows I present CFF values as if a single figure could be assigned to each species. This is a useful simplification, but it glosses over some potentially important complexity. A more careful approach would assign each species a range of values.⁴³ A range of values is more appropriate for three reasons. First, random noise inevitably creeps into experimental results. Second, there is normal variation among individuals of the same species. Third, an animal's life stage sometimes affects its CFF.⁴⁴ Unfortunately, due to time constraints, I have not collected such ranges.⁴⁵ As examples of what such ranges might look like, <u>McComb</u> et al. 2010 report a CFF value of 27.3 ± 3.15 Hz for the scalloped hammerhead shark (*Sphyrna lewini*) and <u>Lisney et al. 2011</u> report a CFF value of 87.0 ± 8.98 Hz for the domestic chicken (*Gallus gallus domesticus*). Given these sorts of ranges, small differences in reported CFF values should not be taken too seriously.

Although CFF values vary considerably across the animal kingdom, our "[u]nderstanding of what drives variation in temporal sensitivity within and between taxa remains poor, beyond the fact that CFFs are related to the light levels to which animals are exposed and tend to scale with metabolic rate and body size" (Inger et al. 2014: 9). Reported CFF values across species span about two orders of magnitude. As a reference point, humans are generally reckoned to have a CFF of around 60 Hz. About two-thirds

of animals that have been studied have CFF thresholds lower than humans.⁴⁶ For instance, the leatherback sea turtle (*Dermochelys coriacea*) has a CFF of ~15 Hz (<u>Healey et al. 2013</u>), the Sergestid shrimp (*Sergia filictum*) has a CFF of ~24 Hz (<u>Frank 2000</u>), the common cuttlefish (*Sepia officinalis*) has a CFF of ~42 Hz (<u>Nelson 2003</u>), and the American crayfish (*Cambarus spp*) has a CFF of ~53 Hz (<u>Inger et al. 2014</u>). About one-third of studied animals have CFF values higher than humans. For instance, the common octopus (*Octopus vulgaris*) has a CFF of ~72 Hz (<u>Hamasaki 1968</u>), the domestic dog (*Canis lupus familiaris*) has a CFF of ~80 Hz (<u>Healey et al. 2013</u>), and the pied flycatcher (a type of small bird, *Ficedula hypoleuca*) has a CFF of ~146 Hz (<u>Boström et al 2016</u>). (See Figure 5.)



Figure 5: The putative effect of CFF on the trajectory of a moving object as perceived by different species. Gray shaded areas represent temporal windows of information integration (source: Jura 2019: 2)⁴⁷

42 Ideal conditions = comparing diurnal mammals or birds that predominantly rely on vision

⁴⁷ This figure, like Figure 1 above, is potentially misleading because it averages motion trajectory without incorporating motion blur. The leatherback turtle doesn't see a motionless target but instead a big blur centered on one location. It's also worth noting that I have chosen not to include the blowfly (*Calliphora erythrocephala*), represented here, in my own spreadsheet because the relevant study is old (<u>Autrum 1949</u>), the reported result is very high (CFF = 265 Hz), and



⁴³ As noted above, CFF thresholds are sensitive to various environmental conditions. However, unless marked otherwise, all CFF values in this post are reported in terms of *maximum* thresholds. At the species level, maximum thresholds should still ideally be reported as a range, due to our inherent uncertainty and normal variation among individuals within a species. However, the appropriate range for a maximum threshold will be much smaller than the total range of values that CFF can take for an individual of a given species in any environmental conditions.

⁴⁴ For instance, <u>Nelson 2003</u> reports a CFF value of 24 Hz for adult cuttlefish (*Sepia officinalis*), but a value of 42 Hz for juveniles of the same species (104). It is unclear to me how common (and how large) CFF variation between life stages is.

⁴⁵ The main issue is that, for the most part, I have collected CFF values from various review articles, which report CFF values as a single figure. Incorporating ranges would require one to look through the individual studies cited in the review articles. Because I don't think adding ranges would add much (current) action-relevant information, I have chosen not to do this (at this time).

⁴⁶ Note that this fact does not entail that two-thirds of all species have CFF values lower than humans. The animals that have been studied thus far are not representative of wider taxa.

I have compiled <u>a spreadsheet</u> comparing CFF values across 70 species and 33 orders of animals (see Figure 6). Green-shaded cells represent animals with higher CFF values than humans; red-shaded cells represent animals with CFF values lower than humans. (Note that the order averages in the second tab can't be interpreted literally because we don't have a representative sampling of the species from the orders.) The spreadsheet combines the values from several review articles as well as individual results from a handful of studies on species of particular interest. The spreadsheet is not intended to be comprehensive. My review of the literature was somewhat cursory, and hence I do not claim that this is an exhaustive list of the animals that have been studied. Nonetheless, I think the spreadsheet does offer a somewhat representative survey of the breadth of animals studied and the range of CFF values recorded.

	Phylum	Class	Order	Species	Common Name	CFF	Source
,	Arthropoda	Malacostraca	Decapoda	Janicella spinicauda	Oplophorid Shrimp	31	Frank 2000
	Arthropoda	Malacostraca	Decapoda	Oplophorus gracilirostris	Oplophorid Shrimp	32	Frank 2000
	Chordata	Mammalia	Carnivora	Pagophilus groenlandicus	Harp Seal	32.7	Healey et al 2013
	Chordata	Chondrichthyes	Carcharhiniformes	Negaprion brevirostris	Lemon Shark	37	Healey et al 2013
	Chordata	Actinopterygii	Beloniformes	Oryzias latipes	Japanese Rice Fish	37.2	Healey et al 2013
	Chordata	Mammalia	Rodentia	Rattus norvegicus	Brown Rat	39	Healey et al 2013
	Chordata	Reptilia	Testudines	Caretta caretta	Loggerhead Sea Turtle	40	Healey et al 2013
	Chordata	Reptilia	Testudines	Chelonia mydas	Green Sea Turtle	40	Healey et al 2013
,	Arthropoda	Malacostraca	Euphausiacea	Stylocheiron maximum	Euphausiid Krill	40	Frank 2000
,	Arthropoda	Arachnida	Araneae	Maevia inclemens	Jumping Spider	40	Inger et al 2014
	Mollusca	Cephalopoda	Sepiida	Sepia officinalis	Common cuttlefish	42	Nelson 2003
	Arthropoda	Insecta	Blattodea	Periplaneta americana	American Cockroach	42.5	Inger et al 2014
,	Arthropoda	Malacostraca	Euphausiacea	Nematobrachion flexipes	Euphausiid Krill	44	Frank 2000
	Chordata	Aves	Strigiformes	Bubo virginianus	Great-Horned Owl	45	Healey et al 2013
	Chordata	Reptilia	Rhynchocephalia	Sphenodon punctatus	Tuatara	45.6	Healey et al 2013
	Chordata	Mammalia	Rodentia	Cavia porcellus	Guinea Pig	50	Healey et al 2013
	Arthropoda	Malacostraca	Decapoda	Cambarus spp	American Crayfish	53	Inger et al 2014
	Arthropoda	Malacostraca	Decapoda	Pagurus spp	Hermit Crab	53	Inger et al 2014
	Chordata	Mammalia	Carnivora	Felis catus	Cat	55	Healey et al 2013
	Arthropoda	Malacostraca	Euphausiacea	Nematobrachion sexspinosus	Euphausiid Krill	56	Frank 2000
	Chordata	Mammalia	Primates	Homo sapiens	Human	60	Healey et al 2013
	Chordata	Mammalia	Rodentia	Tamiasciurus hudsonicus	American Red Squirrel	60	Healey et al 2013
,	Arthropoda	Insecta	Orthoptera	Locusta migratoria	Migratory Locust	65	Inger et al 2014
	Chordata	Actinopterygii	Cypriniformes	Carassius auratus	Goldfish	67	Healey et al 2013
	Chordata	Reptilia	Squamata	Anolis cristatellus	Anolis Lizard	70	Healey et al 2013
	Chordata	Aves	Strigiformes	Asio flammeus	Short-Eared Owl	70	Healey et al 2013
	Arthropoda	Insecta	Lepidoptera	Antheraea pernyi	Chinese Tussah Moth	70	Inger et al 2014
	Mollusca	Cephalopoda	Octopoda	Octopus vulgaris	Common octopus	72	Hamasaki 1968
	Arthropoda	Actinopterygli	Salmoniformes	Salmo salar	Atlantic Salmon	72	Inger et al 2014
	Chordata	Aves	Psittaciformes	Melopsittacus undulatus	Budgerigar	74	Healey et al 2013
	Arthropoda	Insecta	Lepidoptera	Saturnia pavonia	Emperor Moth	75	Inger et al 2014
	Chordata	Mammalia	Carnivora	Canis lupus familiaris	Dog	80	Healey et al 2013
	Chordata	Actinoptervaii	Scombriformes	Thunnus albacares	Yellowfin Tuna	80	Healey et al 2013
	Chordata	Reptilia	Squamata	Iguana iguana	Green Iguana	80	Healey et al 2013
	Arthropoda	Insecta	Diptera	Drosophila hydei	Fruit Fly	80	Incer et al 2014
	Chordata	Aves	Galliformes	Gallus gallus domesticus	Chicken	87	Healey et al 2013
	Chordata	Mammalia	Scandentia	Tupaia glis	Common Treeshrew	90	Healey et al 2013
	Chordata	Mammalia	Primates	Macaca mulatta	Rhesus Macaque	05	Healey et al 2013

Figure 6: Screenshot of <u>CFF spreadsheet</u> (note that the screenshot does not capture the full table)

The spreadsheet offers some somewhat surprising findings. Animals as putatively dissimilar as hermit crabs (~53 Hz), humans (~60 Hz), migratory locusts (~65 Hz), and goldfish (~67 Hz) have roughly similar CFF thresholds. On the other hand, animals as putatively similar as trout (~27 Hz) and salmon (~72 Hz), geckos (~20 Hz) and iguanas (~80 Hz), and guinea pigs (~50 Hz) and ground squirrels (~120 Hz), have drastically different CFF thresholds. Reptiles, insects, fish, and mammals all exhibit tremendous diversity in CFF values,⁴⁸ though much of this diversity is due to differences in the degree to which different animals in these taxa rely on vision, and as such probably doesn't represent variation in the subjective experience of time.

Conclusion

All things considered, I find it somewhat unlikely that critical flicker-fusion frequency will be a useful metric in isolation. However, in combination with other measures of temporal resolution, as well as relevant neurological and behavioral measures, CFF thresholds can potentially help inform our understanding of differences in the subjective experience of time across species. Additional research will help reveal whether differences in CFF correlate with differences in the subjective experience of time, and if so, under what conditions and to what extent.

Studying the circumstances in which humans reliably report alterations in their subjective rate of experience may help us understand differences in the subjective experience of time across species. In particular, it would be helpful to identify circumstances that reliably trigger reports of differences in subjective rate of experience that can be ethically recreated in experimental conditions. Investigating the physiological, neurological, psychophysical, and behavioral changes that accompany reports of differences in the subjective experience of time could help us better understand the neural underpinnings of temporal experience and the empirically measurable metrics that co-vary with reported differences in temporal experience. We could then apply these findings to other types of animals.

Credits

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Works Cited

Arstila, V. (2012). <u>Time slows down during accidents</u>. *Frontiers in Psychology, 3*, 196.

Autrum, H. (1949). <u>Neue versuche zum optischen auflösungsver-</u> <u>mögen fliegender insekten</u>. *Experientia*, **5**(7), 271-277.

<u>Bin</u>kofski, F., & Block, R. A. (1996). <u>Accelerated time experience</u>

the paper is written in German, so it's difficult for me to examine the details of the study.

⁴⁸ Reptiles range from ~15 Hz (leatherback turtle) to ~80 Hz (green iguana). Insects range from ~42.5 Hz (American cockroach) to ~200 Hz (honey bee). Fish range from ~14 Hz (European Eel) to ~80 Hz (yellowfin tuna). Mammals range from ~32.7 Hz (harp seal) to ~120 Hz (golden-mantled ground squirrel).



after left frontal cortex lesion. *Neurocase*, 2(6), 485-493.

Boström, J. E., Dimitrova, M., Canton, C., Håstad, O., Qvarnström, A., & Ödeen, A. (2016). <u>Ultra-rapid vision in birds</u>. *PloS One*, *11*(3), e0151099.

DeRamus, M. L., & Kraft, T. W. (2018). <u>Optimizing ERG Measures of Scotopic and Photopic Critical Flicker Frequency</u>. In Ash J., Anderson R., LaVail M., Bowes Rickman C., Hollyfield J., Grimm C. (eds) *Retinal Degenerative Diseases* (pp. 145-150). Springer, Cham.

Eisen-Enosh, A., Farah, N., Burgansky-Eliash, Z., Polat, U., & Mandel, Y. (2017). <u>Evaluation of critical flicker-fusion frequency</u> <u>measurement methods for the investigation of visual temporal</u> <u>resolution</u>. *Scientific Reports*, 7(1), 1-9.

Fink, M., Ulbrich, P., Churan, J., & Wittmann, M. (2006). <u>Stimu-</u> <u>lus-dependent processing of temporal order</u>. *Behavioural Processes*, *71*(2-3), 344-352.

Frank, T. M. (2000). <u>Temporal resolution in mesopelagic crusta-</u> <u>ceans</u>. *Philosophical Transactions of the Royal Society of London*. *Series B: Biological Sciences*, *355*(1401), 1195-1198.

Hagura, N., Kanai, R., Orgs, G., & Haggard, P. (2012). <u>Ready</u> steady slow: action preparation slows the subjective passage of time. *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), 4399-4406.

Hamasaki, D. I. (1968). <u>The electroretinogram of the intact anes-</u> <u>thetized octopus</u>. *Vision Research*, **8**(3), 247-258.

Harman, E. (2003). <u>The potentiality problem</u>. *Philosophical Studies: An International Journal for Philosophy in the Analytic Tradition*, *114*(1/2), 173-198.

Healy, K., McNally, L., Ruxton, G. D., Cooper, N., & Jackson, A. L. (2013). <u>Metabolic rate and body size are linked with perception of temporal information</u>. *Animal Behaviour*, *86*(4), 685-696.

Holcombe, A. O. (2009). <u>Seeing slow and seeing fast: two limits</u> on perception. *Trends in Cognitive Sciences*, *13*(5), 216-221.

Ibbotson, M. R. (2017). <u>Visual neuroscience: unique neural system for flight stabilization in hummingbirds</u>. *Current Biology*, 27(2), R58-R61.

Inger, R., Bennie, J., Davies, T. W., & Gaston, K. J. (2014). Poten-

tial biological and ecological effects of flickering artificial light. *PloS One*, *9*(5), e98631.

Jura, B. (2019). <u>A mechanism of synaptic clock underlying subjective time perception</u>. *Frontiers in Neuroscience*, *13*, 716.

Jura, B. (2020). <u>Synaptic clock as a neural substrate of consciousness</u>. *arXiv preprint arXiv:2002.07716*.

Lisney, T. J., Rubene, D., Rózsa, J., Løvlie, H., Håstad, O., & Ödeen, A. (2011). <u>Behavioural assessment of flicker fusion frequency in</u> <u>chicken</u> *Gallus gallus domesticus*. *Vision Research*, *51*(12), 1324-1332.

Lu, S., Cai, Y., Shen, M., Zhou, Y., & Han, S. (2012). <u>Alerting and</u> orienting of attention without visual awareness. *Consciousness* and *Cognition*, *21*(2), 928-938.

Maimon, G., Straw, A. D., & Dickinson, M. H. (2008). <u>A simple</u> vision-based algorithm for decision making in flying *Drosophila*. *Current Biology*, *18*(6), 464-470.

Matthews, W. J., & Meck, W. H. (2014). <u>Time perception: the bad</u> <u>news and the good</u>. *Wiley Interdisciplinary Reviews: Cognitive Sci ence*, **5**(4), 429-446.

McComb, D. M., Frank, T. M., Hueter, R. E., & Kajiura, S. M. (2010). <u>Temporal resolution and spectral sensitivity of the visual system of three coastal shark species from different light environments</u>. *Physiological and Biochemical Zoology*, *83*(2), 299-307.

Nelson, L. (2003). <u>An investigation of the phototransduction</u> cascade and temporal characteristics of the retina of the cuttlefish, *Sepia officinalis*. Doctoral thesis.

Pariyadath, V., & Eagleman, D. (2007). <u>The effect of predictabil-</u> <u>ity on subjective duration</u>. *PloS One*, **2**(11), e1264.

Phillips, I. (2013). <u>Perceiving the passing of time</u>. *Proceedings of the Aristotelian Society*. 113(3), 225-252.

Ros, I. G., & Biewener, A. A. (2016). <u>Optic flow stabilizes flight</u> <u>in ruby-throated hummingbirds</u>. *Journal of Experimental Biology*, *219*(16), 2443-2448.

Stetson, C., Fiesta, M. P., & Eagleman, D. M. (2007). <u>Does time</u> really slow down during a frightening event?. *PloS One*, *2*(12), e1295.



Umeton, D., Read, J. C., & Rowe, C. (2017). <u>Unravelling the illusion of flicker fusion</u>. *Biology Letters*, *13*(2), 20160831.

Wilson, D. R., & Hare, J. F. (2004). <u>Ground squirrel uses ultrason-</u> ic alarms. *Nature*, *430*(6999), 523-523.

Wittmann, M. (2016). *Felt Time: The Psychology of How We Perceive Time*. Mit Press.

