Review

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Psychophysics and the evolution of behavior

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Sensory information allows animals to interpret their environment and make decisions. The ways in which animals perceive and measure stimuli from the social and physical environment guide nearly every decision they make. Thus, sensory perception and associated cognitive processing have a strong impact on behavioral evolution. Research in this area often focuses on the unique properties of the sensory system of an individual species, yet certain relevant features of perception and cognition generally hold across taxa. One such general feature is the proportionally based translation of physical stimulus magnitude into perceived stimulus magnitude. This process has been recognized for over a century, but recent studies have begun to consider how a law of proportional psychophysics, Weber's law, exerts selective force in behavioral evolution.

Proportional processing

Perception and cognition filter and process the information animals use to make decisions in every area of their lives. Understanding of animal perception and cognition has led to important discoveries about behavioral evolution [1–5]. Research into the sensory mechanisms of an individual species frequently reveals specialized sensitivity to a particular range of sensory information that explains some aspect of behavior [6,7]. Yet some features of perceptual and cognitive systems are so general that they are shared across sensory systems and across taxa. For example, habituation [8] and generalization [9] guide animal responses to environmental stimuli in ways that shape the evolution of competition and mimicry.

The mechanisms of comparing environmental stimuli are also broadly shared and are critical for decisions based on discrimination, recognition, and matching. These basic types of decisions occur in every area of behavior, so the way in which animals assess and compare stimuli should broadly influence behavioral evolution. Animals, including humans, generally compare stimuli based on proportional rather than absolute differences in stimulus magnitude [10,11]. For example, if you wanted to secretly take a cookie from a dessert table, intuitively you would take one from a tray piled high with 100 cookies rather than a tray that holds just ten cookies. Cookie removal would be more easily detected from a smaller quantity. This is because the nervous system notices the proportional difference in cookie quantity (1/100 is smaller than 1/10). If the absolute difference, equal to 1 in both cases (100 – 99 = 1 and 10 – 9 = 1), were the primary influence on the decision, taking a cookie from either tray would have the same impact. Weber's law describes the ability of a sensory system to distinguish between two stimulus magnitudes based on their proportional difference (Box 1). When sensory systems adhere to Weber's law, hereafter termed proportional processing, the smallest change that can be detected is a constant proportion of stimulus magnitude. For example, if we can detect a proportional change of one-tenth in cookie-pile magnitude, removal of ten cookies from the pile of 100 would allow us to detect the change.

Animals use proportional processing to detect changes in sound, light, odors, electrical fields, pressure, number, and time (Table 1). Not all sensory parameters are detected in this way. Proportional processing is generally thought to help sensory systems in reducing the enormous variation in magnitude that can occur within one sensory parameter. For example, light levels vary by over ten orders of magnitude from a moonless night to a sunlit day [12]. Sensory cells can communicate such differences efficiently by compressing the variation into a logarithmic scale, and this appears to be the root of Weber's law [13]. Most proportional processing research focuses on humans, but many taxa, including invertebrates [14–17] and perhaps even bacteria [18,19], adhere to Weber's law.

The widespread occurrence of proportional processing indicates that it influences the evolution of behavior in most animals. In this review we show how proportional processing affects five types of comparison used in decision-making. For each comparison we use examples to predict how proportional processing might have evolutionary

Glossary

Absolute difference: value calculated by subtracting one stimulus magnitude from another.
Discrimination: task in which an animal compares two stimulus values to determine whether they are different.
Discrimination threshold: smallest increment of difference in magnitude that can be detected by a sensory system.
Proportional difference: ratio of the difference between stimulus magnitudes and the magnitude of one of the stimuli.
Proportional processing: decision-making process in which an animal compares stimulus values according to their proportional difference in adherence with Weber's law.
Recognition: task in which an animal compares a variable environmental stimulus value to a pre-existing neural template value.

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Box 1. Defining Weber's law

Many animal decisions depend on an ability to discriminate between stimulus magnitudes. For example, some females prefer longer male vocalizations and many individuals prefer larger food items. If animals perceive the absolute difference between two stimuli, correct choice of the greater stimulus becomes more difficult as the difference between them approaches zero, regardless of their magnitude. If animals perceive the proportional difference between two stimuli, correct choice of the greater stimulus becomes more difficult as their ratio approaches 1, regardless of their magnitude. When animals adhere to Weber's law, they compare stimuli on the basis of proportional differences. For example, human visual perception of the difference between two dot clusters depends on proportional rather than absolute differences. At small magnitudes, an absolute difference of 1 dot (proportional difference = 1/6) is sufficient to notice a difference (Figure IA). At larger magnitudes, an absolute difference of 1 dot (Figure IB, right; proportional difference of upper = 1/12, lower = 1/36) is difficult to detect, but the proportional difference of 1/6 (left) is still readily seen.

Weber's law is expressed formally as $\Delta I = kI$, where ΔI is the minimum detectable change in a stimulus of magnitude I and k is a constant [11]. The constant k is often called the Weber fraction. For example, the Weber fraction for human contrast vision is approximately 0.01. This formula guides research in many fields, but there is some variation in how people define I. Weber's law compares two stimuli, S_1 and S_2, that differ by ΔI. Vision studies usually define I as the background stimulus S_1, and S_2 as an object seen against the background [12]. Hearing studies usually define I as the smaller [66] or greater [67] of S_1 and S_2. The difference rarely affects important conclusions, but for some predictions it matters. We point out where this occurs.

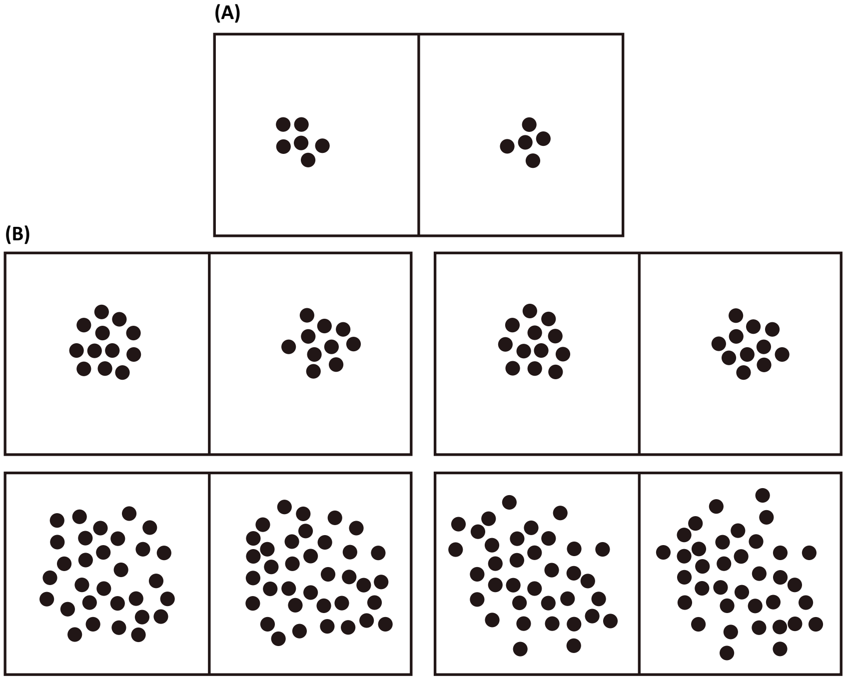

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Figure I. Discriminating between dot clusters is easier when the proportional difference between stimuli is large. **(A)** Proportional difference = 1/6, absolute difference = 1. **(B)** On the left, the proportional difference remains 1/6. On the right, the absolute difference remains 1, but the proportional difference decreases (upper = 1/12 and lower = 1/36).

consequences in the hope that readers will apply the concept in novel ways. We then briefly discuss how Weber's law is just one aspect of the salience of proportions in the nervous system, and suggest that proportional processing might have played a role in the evolution of broad cognitive domains such as music and mathematics. Finally, we discuss how future research will improve our understanding of the evolutionary consequences of proportional processing.

Evolutionary consequences for behavior

When sensory systems translate a physical stimulus into a perceived one, they do not measure the magnitude exactly. A discrimination threshold leaves small increments of change undetected. For example, most people, unless they count, do not detect one cookie removed from 100 because this change is less than the discrimination threshold. Every sensory parameter that animals can detect has a discrimination threshold. Because of this, animals can fail to detect some increments of change that might be relevant to decisions. With proportional processing, undetected increments are small at low magnitudes and large at high magnitudes, which leads to specific predictions about behavioral evolution [20–22]. In these cases, animals can more easily detect a given absolute change at lower than at higher magnitudes (1 cookie from 10 rather than from 100). In addition, in these cases animals can more accurately identify a stimulus value at low magnitude, and they can more easily discriminate between two stimuli if they are low in magnitude.

Proportional processing can influence decisions that depend on a variety of comparisons. Here we discuss detecting change, matching behavioral output to a stimulus value, discriminating between stimuli, recognizing when a stimulus matches a neural template, and remembering the probability of reward outcomes. The precise sensory parameter measured when a species responds to natural multiparameter stimuli is not always clear, and

Table 1. The sensory modalities of Weber's law

Sensory modality	Sensory parameter[a]	Adherence range	Departure range	Taxonomic groups tested	Refs
Hearing	Amplitude	Broadband noise played to be 10–80 dB SPL re 20 μPa at the ear[b]	Discrimination improves as intensity increases for tonal sounds	Humans, birds, mammals	[66,68]
		Played at variable levels for vocal signals	For insects and anurans, discrimination worsens as intensity increases	Insects, anurans	[17,68,69]
	Frequency	Depends on amplitude, occurs at intermediate range (~300–2000 Hz)	Discrimination at higher frequencies worsens as frequency increases	Humans, parakeets	[66,70]
Vision	Area	Quantities tested vary	Quantities tested vary	Coyotes, humans, seals	[58,71,72]
	Intensity	Varies with taxon; some photopic levels for humans	Varies with taxon; scotopic levels and high photopic levels for humans	Humans, many others	[73]
	Wavelength	Predicted but not shown in mantis shrimp (owing to unique photoreceptors)	Generally does not occur owing to the mechanism of detection	Humans, goldfish, honeybees, butterflies	[12,74]
Approximate number sense	Nonsymbolic assessment of quantity	Quantities tested vary	Quantities tested vary	Humans, monkeys, fish, chimps, crows	[13,34,35, 58–61,75,76]
Time, duration	Time interval passed (acoustic and visual modalities)	Evidence of multiple ranges; Weber fraction changes between ranges	Evidence against some ranges; depends on measurement method [77] and stimulus details [67]	Parasites, humans, pigeons, starlings	[16,78–80] but see [81–83]
Magnetoreception	Intensity	Predicted not to occur: the intensity of the Earth's magnetic field varies by a factor of only two			
	Inclination angle	Predicted not to occur: the inclination angle of the Earth's magnetic field only ranges from –90° to 90°			
Chemoreception	Concentration	Quantities tested vary	Quantities tested vary, but evidence that discrimination improves with increasing intensity, as for sound amplitude discrimination	Bats, bees, ants, bacteria	[14,15,18,19, 37,84]
Tactile sense	Pressure	Tested with detection of weights up to 32 oz	Not tested in other ranges	Humans	[10]
	Vibrotactile frequency	Below 50 Hz	Not tested in other ranges	Humans, primates	[85,86]
	Edge sharpness	40°–90°	Not tested in other ranges	Humans	[87]
Electroreception	Intensity	For distance-relevant voltage–amplitude changes detected from electrolocation		Weakly electric fish	[88]

[a] In some cases in which behavior adheres to Weber's law, the relevant sensory parameter is not clear. For example, starling memory of food amount could be based on sensory cues including the number of units, weight, caloric content, time of consumption, or other factors [43]. In response to communication signals that vary in the number of elements, animals might respond to total acoustic energy, call duration, or number [30].

[b] SPL, sound pressure level.

this can dramatically change the evolutionary consequences. For example, animals responding to vocalizations could assess duration, intensity, frequency, total energy, pulse rate, intercall interval, or all these features. In addition, sensory systems might evolve so that discrimination thresholds change rather than cause behavior to change. Nevertheless, considering the role of proportional processing might be a powerful tool in understanding behavioral evolution.

Detecting change

When the discrimination threshold is a constant proportion of the stimulus magnitude, the detectable increment of change is magnitude-dependent (Box 2, Figure I). Thus, use of proportional processing might influence behaviors based on detection of change. For example, we predict that proportional processing might be one of several factors influencing the evolution of brood parasitism. Some brood parasites lay one egg per host nest [23]. This egg is more likely to hatch and fledge if the hosts do not detect it, otherwise they might eject it or abandon the nest. Hosts may detect additional eggs via an approximate number sense or a visually measured spatial area, each of which is proportionally processed in a variety of taxa. Brood parasites might improve fitness by preferentially targeting larger clutches, among which one additional egg would be harder to detect. In addition, depending on brood parasite abundance and the opportunity to lay multiple clutches, hosts might improve fitness by laying fewer eggs at a time. Smaller clutches would make nests less attractive to brood parasites that target larger clutches and make it easier to detect an additional egg.

Matching behavioral output to a stimulus value

Within the range of sensitivity that follows Weber's law, higher-magnitude stimuli are more difficult to measure accurately because accuracy can only occur within the window of the discrimination threshold (Box 2, Figure I). This can influence decisions in which animals match the magnitude of a behavioral output to a fixed stimulus value. For example, animals that navigate by path integration use outgoing path information to calculate a straight-line return path to home. They must match behavioral output (walking the homebound path) to this fixed, straight-line path value [24]. If animals have a proportional error in matching these values, the absolute error in distance will increase with the path length. This should limit the distance an animal can travel, because the error would eventually be so large that the individual could not find home. This could select for the evolution of new navigation strategies to cover the distance of a potential error. In fact, desert ants show increased absolute errors after longer foraging routes and use a separate navigation technique when close to home [25].

Discriminating between stimuli

Animals frequently compare two or more stimuli to make a choice, such as in choosing a mate or a meal. Choosing between stimuli depends on noticing a difference between them. With proportional processing, the minimum detectable increment is greater when comparing high-magnitude stimuli (Box 2, Figure III). This should be especially relevant to decisions for which time-dependent costs limit how long an animal can spend in assessing options [26,27]. When discrimination becomes harder as stimuli become larger, individuals might not discriminate between stimuli

Box 2. Three types of decision influenced by proportional processing

Proportional processing influences many decisions, but the type of influence varies. Three possible types of influence include (i) magnitude-dependent detection of change, (ii) a greater minimum noticeable increment at high magnitudes, and (iii) an asymmetric error in recognizing a stimulus. Here we show general representations of how stimuli are compared in these three cases, with examples of how each comparison could influence a natural animal behavior. The axis represents variation in a sensory parameter from low to high magnitude, with equal linear increments marked. Thick vertical lines represent stimuli. Brackets denote the amount of change required to notice a difference from a particular point of stimulus variation.

Magnitude-dependent detection of change

Figure I shows a representation of magnitude-dependent detection of change.

Example If the egg of a brood parasite is detected, the host might try to remove it or abandon the nest (Figure II). If birds detect a change in clutch size via proportional processing, they will be more likely to notice one egg if the original clutch is smaller. In this case, brood parasites would be more successful if they preferentially parasitized larger clutches. Hosts would be more successful if they produced smaller clutches.

Greater minimum noticeable increment at high magnitudes

Figure III shows a representation of a greater minimum noticeable increment at high magnitudes.

Example If females choose to mate with males that have longer tails, the same increment difference would be harder to discriminate between longer tails (Figure IV). This could stimulate the evolution of a new trait to aid in female attraction.

Asymmetric error in recognizing a stimulus

Figure V shows a representation of an asymmetric error in recognizing a stimulus.

Example If two sister species move into sympatry, they might have overlapping ranges of mate attraction call rates (Figure VI). To evolve call differences that will avoid costly hybridization, one species must shift their range. If all other factors are equal, shifting to the lower rather than higher range will more quickly allow accurate female recognition.

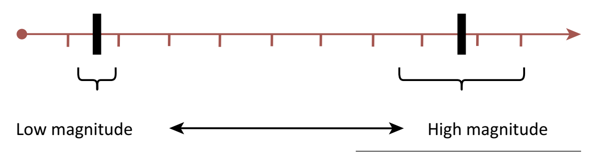

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Figure I. With proportional processing, detecting a certain increment of change is easier at low magnitude.

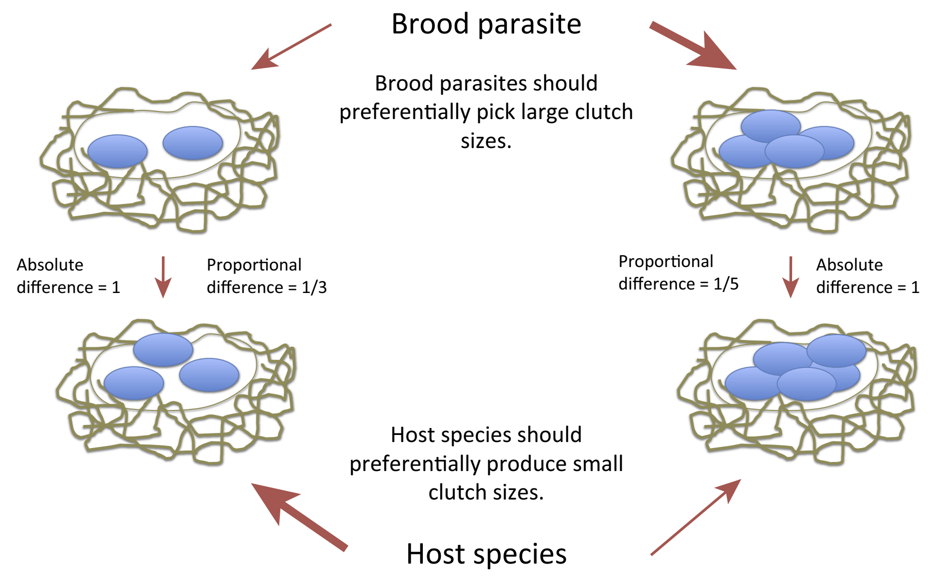

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Figure II. Proportional processing might influence the evolution of brood parasites and their hosts.

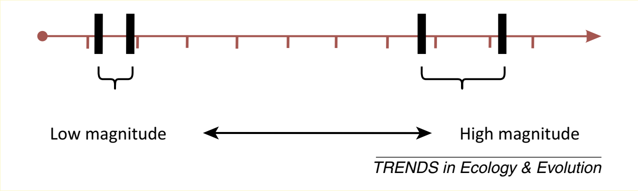

Figure III. With proportional processing, a smaller difference can be discriminated at lower magnitudes.

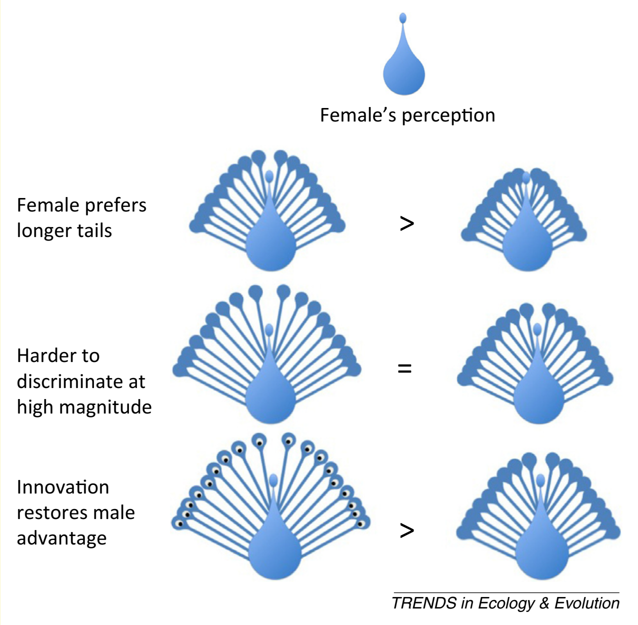

Figure IV. Proportional processing could influence the evolution of sexually selected male traits.

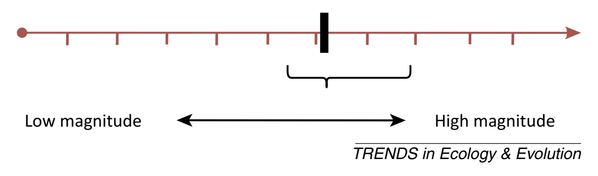

Figure V. With proportional processing, the discrimination threshold could be smaller in the direction of lower magnitude.

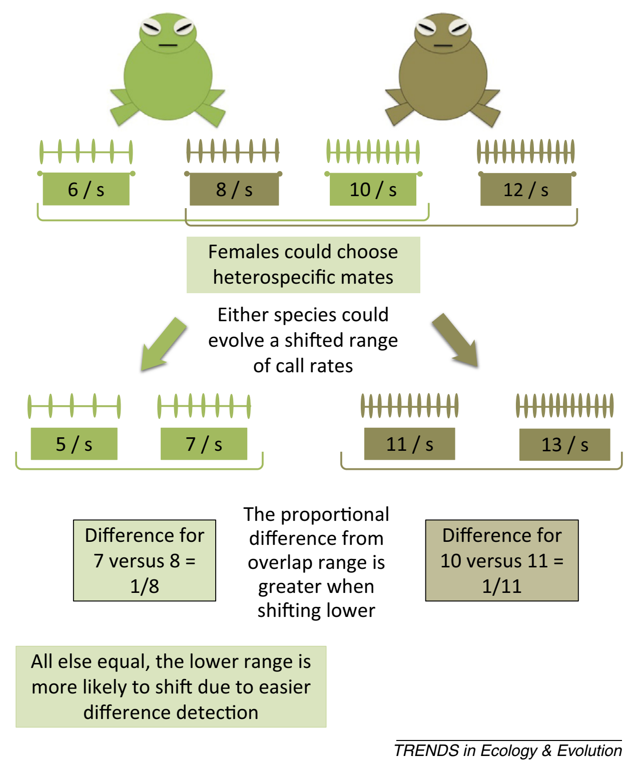

Figure VI. Proportional processing could influence the evolution of character displacement in closely related species.

above a certain magnitude. For example, proportional processing might limit the evolutionary process of increasing the magnitude of male traits through sexual selection because eventually females cannot easily notice an additional increase in magnitude (for duration, number of elements, length, etc.) [21,28–30]. Especially when the cost of producing greater trait intensity increases linearly with trait magnitude, the cost-to-benefit ratio of increasing trait magnitude quickly becomes unfavorable for males. At this point, males might evolve new traits to increase female attraction [30,31].

Proportional processing by different types of signal receivers will exert variable selective forces on signal evolution. For example, when predators base attack decisions on prey communication signals, with preferential attack on individuals that produce higher-magnitude signals, predators can limit the evolution of increasing magnitude in sexual signals. However, when predators use proportional processing to discriminate signal magnitude, they will be unable to discriminate at high magnitudes and might no longer select against the evolution of increasing signal magnitude [30].

Proportional processing might influence behavioral escalation. Males that compete by using dynamic signals should have more difficulty assessing competition when signals escalate to high magnitudes, such as getting louder or longer. Thus, males should increase signal magnitude by ever greater increments as competition escalates to ensure that receivers can detect the increase.

Proportional processing of static male traits, such as saturated plumage coloration, could also influence competition by widening the range of trait variation perceived as threatening by the most attractive (high magnitude) males. If males and females cannot easily discriminate between intermediate- and high-magnitude males and trait magnitude correlates with ability to win contests, high-magnitude males will win contests with intermediate-magnitude males, but will not bother to fight low-magnitude males. This could dramatically reduce access by intermediate-magnitude males to females and leave low-magnitude males free of competition, imposing disruptive selection on trait magnitude. This behavioral pattern occurs in Lazuli buntings, although a role for proportional processing has not been tested. In Lazuli buntings, the bluest males have high reproductive success, the dullest have moderate success, and intermediate males have low success because the bluest males allow only dull males to nest nearby [32].

Several species assess group size via proportional processing when deciding which group to join [33–35]. In these cases, factors such as such as proximity to shelter, food, and mates might play a greater role in decisions when joining large groups.

Recognizing when a stimulus matches a neural template

When sensory systems treat either the smaller or larger of two stimuli being compared as the baseline stimulus (Box 1), there will be different discrimination thresholds on either side of one stimulus value. The discrimination threshold on the lower-magnitude side will be smaller than that on the higher-magnitude side (Box 2, Figure V). This asymmetry could influence decisions in which individuals compare a variable sample stimulus to a fixed target. For example, an asymmetric recognition error could influence reproductive character displacement between sympatric sister species. Suppose two species have call rates of 6–10 pulses/s and 8–12 pulses/s, and females measure call rates to identify species-appropriate mates. If these species merge into sympatry, females of both species will recognize some heterospecifics as mates. Costly hybridization could select for male evolution of different call rates and female preference should diverge. If variability in call rate occurs randomly in both directions, females that use proportional processing would more easily discriminate males that lower their call rate from the overlap range. Males that changed their call rate by the same small increment either above or below the overlap range would be more likely to exceed a discrimination threshold by moving below (Box 2, Figure VI).

An asymmetric recognition error could influence directional evolution when animals experience selection to evolve a difference from a given trait value. For example, animals will improve the efficacy of communication when signals evolve to differ from noise. Discrimination of a signal from noise should occur more quickly if signals evolve toward lower magnitude. For example, within the frequencies discriminated by Weber's law, acoustic signals should stand out from noise more easily if the pitch is lowered rather than raised relative to the noise frequencies. The reverse would be true when animals want to avoid detection by matching a target stimulus value. For example, animals that mimic poisonous species or camouflage themselves via background matching should be more successful if small differences from the target value (e.g., brightness or size) occur in the direction of higher magnitude.

Remembering variable reward outcomes over time

Some behaviors lead to immediate reward outcomes, and proportional processing can influence how animals assess reward magnitude. Pollinators use proportional processing to decide between nectar volume rewards [14,36,37]. If nectar production is costly, pollinator proportional processing should limit the evolution of increasing nectar reward, and might lead to innovation of other attractive plant traits, such as showy flowers and odors. Immediate reward outcomes influence behavior differently than the delayed fitness benefits that often result from responding to stimuli such as mating signals. Pollinators can learn from experience which choices provide the best outcome. Showy visual and olfactory floral traits might evolve to facilitate the association between nectar reward and plant species – not as a consequence of proportional processing. In some cases, flower appearance has a greater influence on pollinator choice than nectar reward [38], and pollinators appear to be subject to the same biases towards exaggerated traits as sexually selective females are [39]. Thus, it is possible that proportional processing by pollinators has influenced the evolution of showy floral traits.

Experience can help animals to improve their decisions if they retain information about the rewards associated with each option in a choice. When animals encounter a particular object or event repeatedly over time, they remember it in association with the probability of receiving a range of possible rewards. For example, if you receive $10 each time you press a green button, you associate that button with a $10 reward. If you receive $8 half the time you press a red button and $12 the other half of the time, you associate that button with a variable probability-based outcome. Assessing reward value can only be as precise as the range of magnitudes within a discrimination threshold. Because of this, proportional processing affects memory of the probability that each option results in a particular reward [22,40,41]. This process was originally presented in the context of scalar utility theory, which describes the processing of information about time [42] and has been successfully applied to other types of information processing [41]. If an option always results in the same reward, an individual associates that option and reward value with high probability distributed over the range of reward values that cannot be distinguished because of the discrimination threshold. If an option results in variable reward values, an individual associates that option with the distributed probability of each outcome, plus or minus variation that cannot be distinguished. With proportional processing, discrimination thresholds are smaller for low-magnitude rewards. There is a narrower range of values over which probability is distributed for the lower reward, so the probability of the actual reward value appears higher. Because of this, memory for variable reward outcomes results in a biased probability function that makes the low-magnitude outcome appear more likely (Figure 1).

Proportional processing influences starling memory of food quantity, as predicted by this understanding of probability-based memory [13,43]. This work has been applied to understanding decisions to avoid or take risks when choosing between rewards [22,40,44,45]. If the reward is desirable, animals given a choice between a constant mid-range reward and a variable low- and high-magnitude reward (equal rewards on average) are less likely to choose variable rewards. However, if the reward outcome is undesirable, animals choose the variable outcomes because memory underestimates the most likely outcome. For example, in the previous button example, the perceived probability of getting $8 on pushing the variable red button

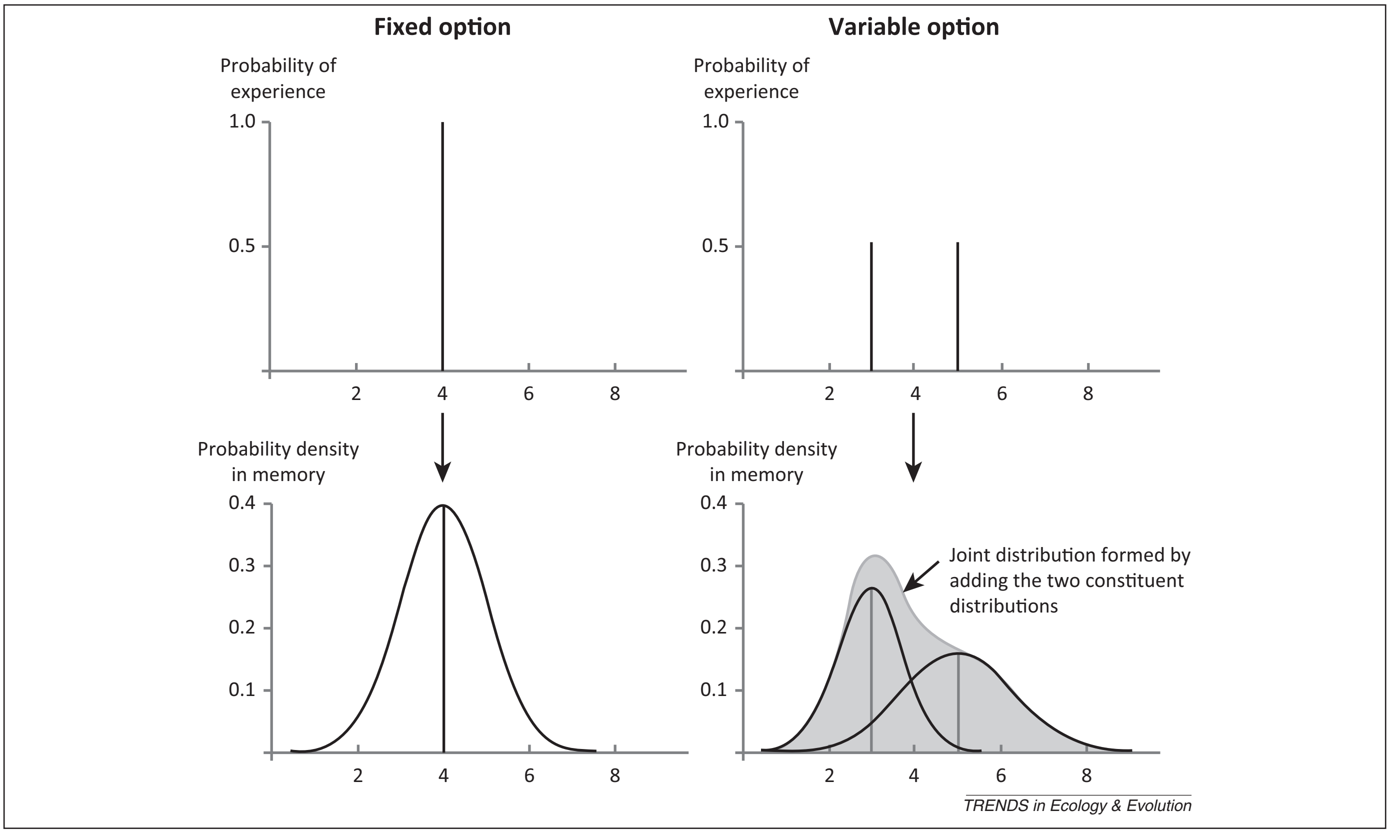

Figure 1. Proportional processing can influence the perceived probability of variable outcomes in a decision. Top left: The probability of experiencing a fixed reward outcome of value 4 is 100%. Top right: The probability of experiencing a variable reward outcome of value 3 or 5 encountered at equal rates is 50% for each. Bottom left: The perceived probability of experiencing the fixed reward outcome is not fixed, but varies within the discrimination threshold for that value. Thus, the perceived probability for value 4 is diluted to less than 100%, but the total probability area under the curve is a distributed 100%. Bottom right: The perceived probability of experiencing each variable reward outcome also varies with the discrimination thresholds for those values. Thus, the perceived probability for both value 3 and 5 is diluted from 50%. Each resulting perceived probability curve is a distributed 50%, but the higher-magnitude reward is distributed over a greater range of magnitudes because of the greater discrimination threshold for proportional processing. Even when the two curves are summed (shaded area) for one cohesive memory associated with the variable option, the peak probability occurs at value 3, and value 3 is perceived as more probable than value 5. Reproduced, with permission, from John Wiley & Sons [40].

is positively biased, and over time people perceive the green button as the better option. However, if both buttons give $10 but differ in a fixed versus a variable delay before payoff, over time people perceive the variable outcome as the better choice because they remember the variable option with a bias toward the shorter waiting time.

These predictions have been supported [46] but are rarely applied outside of foraging [44]. Observers who assess the probability of the variable behavior of an animal could influence the costs and benefits of being consistent. For example, some male fish fan their tails to care for eggs and increase the fanning rate to attract females [47]. If females assess males over time, prefer high fanning rates, and pick the 'most probable rate' (rather than the peak or average rate), males might be more successful with consistent mid-level fanning rates rather than inconsistent high and low rates with equal averages. This is because females could assess the most probable rate as lower for variable males.

A Weber-wired mind

Weber's law describes stimulus assessment in many sensory parameters. The salience of proportional relationships is deeply embedded in our sensory systems, and extends even beyond Weber's law. For example, the proportional relationship between the brightness of a stimulus and its discrimination threshold is constant (adhering to Weber's law) over only a portion of the range of perceptible magnitudes, but outside this range the relationship is still a proportion, just one that gradually shifts [12]. Recent work also suggests that proportional processing influences learning [48–50] and memory [13,43,49]. Thus, Weber's law appears to be a feature not only of perception but also of several cognitive processes [13] (see [51] for an alternative discussion). A nervous system that has evolved to detect proportional relationships might have resulted in a general Weber wiring that influenced the evolution of broad cognitive domains such as music and mathematics.

Music

The importance of proportional relationships is an organizational factor in human musicality, not in terms of detecting differences between stimuli but in assigning importance to stimulus relationships. Music systems are based on octave relationships between frequencies. An octave is defined as two tones with a 2:1 frequency ratio. Other important note relationships in music vary between cultural music systems, but the relevant intervals are always defined by proportional relationships that can be repeated within different octaves [52]. A perfect fifth, for example, has a 3:2 relationship. Thus, music is a collection of consistent ratio relationships for which absolute

Box 3. Proportional sensory scene analysis

Weber's law influences the way we define our sensory surroundings. Visual scene analysis identifies objects from an individual's visual surroundings and defines their relationships. Similarly, auditory scene analysis defines sounds and their relationships in an individual's auditory surroundings. All our sensory systems help us break a dense wall of sensory information into meaningful units. Given our heavily visual perception of the world, we are familiar with the idea of defining visual objects. We do this by attending to shape and brightness contrast rather than to object size. Size changes with distance, but shape and brightness contrast remain constant with distance, and brightness contrast remains constant even as the viewing angle changes. Defining objects by constant proportional relationships is another hallmark of the Weber wiring in our brains.

In the pair of images in Figure I, the absolute radiance difference between the inner and outer squares is the same for the left and right images. However, on the right it is nearly impossible to see the darker inner square because proportionally it is not that different. The contrast is –0.54 on the left and –0.0095 on the right. We would be unlikely to think of these images as the same object under different lighting; rather, they appear to be two different objects.

The same thing happens in auditory scene analysis and nowhere is this more clear than in music. A melody is made up of proportionally related tone intervals. If we transfer a melody up an octave or two but retain the same absolute differences in frequency that related the notes of the original melody, a familiar song becomes unrecognizable and nonmusical because all the intervals are compressed in a small range of frequencies (see the audio files in the supplementary material online).

This might happen in other sensory modalities as well. Panda pheromones differ between males and females according to the proportional content of the odor components [89]. Thus, at any concentration, the difference between male and female pheromones should be retained in the signal by relative proportions. However, this is not a common feature of olfactory signals [90], which can break down over long distances, with each component degrading at its own rate.

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Figure I. The absolute radiance differences between the inner and outer squares are the same on the left and right, but the contrast is obviously different. In fact, it is hard to even see the inner square on the right. This demonstration is most accurate when viewed on a standard sRGB monitor.

frequency differences have no relevance (listen to the audio files in the supplementary material online).

Weber's law simply defined does not directly apply to music, because a frequency discrimination threshold defined by Weber's law is not relevant: note intervals are greater than our discrimination threshold. Rather, the salience of proportional relationships is relevant to music. Music plays with collections of ratio relationships that our brains respond to emotionally [53], perhaps resulting from the similarity of music to the human voice structure [52]. The mathematical formula for Weber's law (Box 1) can define each relationship. For example, an octave = $2I$. A perfect fifth = $1.5I$. Our capacity to recognize these proportional stimulus relationships might relate to Weber's law, or a different proportion-focused feature of our brains (Box 3). Some non-human primates also show a unique response to octave relationships, despite lacking a music faculty [54]. The Weber wiring of brains predates the evolution of music, and might be one of several rudimentary factors that build human musicality [55,56].

Mathematics

A Weber-wired brain that assigns importance to proportional relationships also appears to influence our use of mathematics. Humans and several other vertebrates have a nonsymbolic numerical sense [57] called the approximate number system (ANS) that allows a nonverbal approximate assessment of object quantity and adheres to Weber's law [20,58–60]. The ANS is distinguished from a modality-specific quantity comparator because the nonverbal numerical representation can hold when passed between sensory modalities [61]. Learning of symbolic number representations releases people from depending on proportional comparisons that make high-magnitude assessment inexact [62]. Without a verbal representation of number, a problem such as discriminating 1 000 000 from 1 000 001 of anything would be impossible. Release from proportional numerical comparisons has had a stunning impact on our cultural trajectory [20]. Yet the ANS seems cognitively tied to our system of formal mathematics.

Formal mathematics allows individuals to do far more than compare quantities. Much of mathematics depends on abstract thinking that is hard to tie to sensory perception. Yet formal mathematics revolves around assessment of number intervals, and the relationship between formal mathematics and our Weber-wired brains is fascinating, if foggy [63–65]. Some relationships relevant to mathematics can be defined by the Weber's law equation. An equilateral triangle can be defined as 'each angle = 1/3(total)'. Such equations hardly build the calculations of abstract mathematics. Nevertheless, studies suggest a connection between the ANS and abstract calculations. Cultures with no formal mathematics or symbolic numbers can conduct simple division [64]. In addition, arithmetic scores strongly correlate with ANS discrimination ability, whereas geometry scores strongly correlate with the ability to discriminate spatial area [58]. This suggests that abstract cognition is somehow tied to sensory processes.

Future research

Although the use of proportional processing by animals has been extensively documented, its influence on behavioral evolution has rarely been tested. Thus, it is not yet clear how much broad adherence to Weber's law matters for behavioral evolution. To understand this, researchers must first recognize where these consequences might lie, as outlined in this review. The next step is to model what behavior influenced by proportional processing would look like, and to test whether behavioral patterns match these models. It will be challenging, however, to determine when proportional processing is responsible for behaviors that match models. Many selective forces contribute to behavioral evolution, and other factors could cause the same behavioral patterns predicted by proportional processing.

We suggest three ways to address this problem, building on previous consideration of the issue [30]. (i) Examination of the most obvious alternative explanations might show that those factors would result in a different pattern, increasing the probability that proportional processing causes observed patterns. For example, animals might attend to absolute differences, or base decisions on measureable fitness benefits. (ii) By solving for the *k* value that would lead to the behavioral patterns observed, researchers can test whether the same *k* value underlies a separate task based on discriminating along the same sensory parameter. If so, this increases the probability that proportional processing causes the patterns observed. (iii) If multiple species respond to the same stimuli for different reasons, their fitness benefits likely scale differently with stimulus variation. If multiple species respond with the same *k* value, it is unlikely that the response is determined by fitness benefits, and this increases the probability that they act under the constraints of proportional processing.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tree.2014.03.007.

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