A SOCIO-ECOLOGICAL APPROACH TO PERCEPTION

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Our conscious visual experience of the environment is derived from optical information consisting of an ever-changing distribution of light specified in angular units. To transform these units into linear spatial units appropriate for the specification of spatial extents, the visual system needs geometry and a ruler to scale the information. We review the evidence that perceptual rulers derive from the body's phenotype, which is comprised of our morphology, physiology, and behavioral repertoire. We then propose that perception is also scaled relative to the socio-ecological environment. In this account, social resources affect perception by extending or contracting the relevant physiological ruler. Additionally, we suggest the human ecology functions to select the relevant perceptual ruler. Finally, we highlight research on individual differences as a useful method to further investigate these issues. In moving forward, a complete account of visual perception must necessarily include the socio-ecological environment.

Key words: visual perception, social resources, perceptual scaling, socio-ecological environment

The information for visual perception consists of optic flow and ocular-motor adjustments, both of which consist of angular units. In order to transform these angular units into linear units appropriate for the perception of distance and size, the visual system must make use of geometry and rulers. Our embodied approach to perception contends that the body's phenotype, consisting of morphology, physiology, and behavior, provides the rulers by which spatial perceptions are scaled (Proffitt & Linkenauger, 2013). Depending on one's goals in a particular environment, different aspects of the body become relevant perceptual rulers. Picking up an object, for example, makes hand size relevant, whereas reaching to a location implicates arm's length. In the current paper, we review our embodied approach to perception, and in particular, discuss how walkable extents are scaled to the physiological resources required to traverse the extent. We then consider how social resources function to augment or deplete the resources available for locomotion, and thereby, contribute to the scaling of walkable extents. Given the inherent variability in peoples' phenotypes, we favor an individual differences approach to investigating socio-ecological effects in perception.

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THE BODY AS A PERCEPTUAL RULER

Visual information consists of the angular distribution of light at a point of observation. As individuals move in the environment, this angular distribution changes in a lawful way, called optic flow, which specifies the spatial layout of the environment (Gibson, 1979). A useful animation demonstrating this point can be viewed at <http://www.faculty.virginia.edu/perlab/misc/bookanimations/>. The visual system's use of this information is twofold; it informs the visual guidance of action and is the basis for explicit perceptual experience. There is evidence that the visual system acts directly on changes in visual angles to guide action (for a review, see Fajen, 2007; van der Kamp, Oudejans, & Savelsbergh, 2003). However, our explicit perceptual experience cannot be comprised in these angular units. Instead, the optic flow must be transformed into linear units appropriate for specifying size and extent. The geometrical manner by which optical information is transformed into apparent size and distance has been studied extensively (Proffitt & Caudek, 2013). How this information has been scaled has been studied less; however, existing accounts point to the body as providing the effective perceptual rulers (Proffitt, 2006; Proffitt & Linkenauger, 2013). We know of no solution to the scaling problem that does not rely on the body.

A seminal example of how the body can serve as a perceptual ruler was provided by Sedgwick (1986), who demonstrated how the observer's eye-height can be used to calculate the heights of objects. When gazing straight ahead in the environment, the observer's line of sight corresponds to the horizon line; the height of any object where it intersects the horizon line is the same as the perceiver's eye-height. For example, suppose Bob's eye-height is 6 feet and he is looking at a pole that extends above the horizon line. The height from the bottom of the pole to the horizon line corresponds to Bob's eye-height, and so it is 6 feet. As illustrated in Fig. 1, the total height of the pole can be calculated as the ratio A/B , where A is the height from the top of the pole to the horizon and B is the height from the bottom of the pole to the horizon. Thus, B always corresponds to the eye-height of the perceiver. Determining the height of the pole requires a simple calculation of the proportion from the top of the pole to the horizon (A) relative to the perceiver's eye height (B). For example, if $1/2$ of the pole Bob is seeing extends above the horizon, the height ratio of A to B is $1 : 1$. Since we know Bob's eye height is 6 feet, the height of the pole extending below the horizon is 6 feet, the height of the pole extending above the horizon must also be 6 feet, and thus, the height of the entire pole is 12 feet. Interestingly, if Suzy's eye-height is shorter than Bob's, her A/B ratio will be larger. For example, if Suzy's eye-height is 4 feet, then Suzy sees $2/3$ of the same pole as extending above the horizon. Therefore, her horizon ratio is $2 : 1$. For Suzy, the height of the pole below the horizon (B) is 4 feet and the height of the pole above the horizon (A) is 8 feet. Suzy will perceive the pole as much bigger than does Bob because her ruler, her eye-height, is smaller (see Fig. 2).

Eye-height alone, however, has limited utility (Proffitt, 2013; Wraga & Proffitt, 2000). For example, the utility of eye-height is limited to situations where both the observer and the target object are stationed at ground level and the ground plane between the observer and the object is relatively flat. Moreover, eye-height is neither useful for scaling the size of a coffee cup on a table nor the distance to objects much beyond 20 meters. Eye-height

Fig. 1. In the above figure, the yellow horizontal line represents the horizon. The height of the pole can be calculated as the ratio A/B . A is the height from the top of the pole to the horizon and B is the height from the bottom of the pole to the horizon, which corresponds to the perceiver's eye-height.¹

Fig. 2. For both Bob (right) and Sue (left), the horizon corresponds to the perceiver's eye-height. Since Sue is shorter than Bob, the proportion of the pole extending above the horizon (A) is larger. Her perceptual ruler, her eye-height, is smaller and so she perceives the same pole to be bigger than Bob.¹

is useful in certain situations, but in others different perceptual rules must be applied. These rulers derive from the body's phenotype; where a phenotype is comprised of the body's morphology, physiology, and behavioral repertoire (Proffitt & Linkenauger, 2013). The aspect of the phenotype that is selected to serve as the perceptual ruler depends on what is relevant for acting in the environment. If Sue is thirsty and needs a sip of water to drink, what becomes relevant is whether or not the bottled water in front of her is reachable.

¹ This figure was originally published in Proffitt & Linkenauger, 2013.

In this situation, her visual perception of the distance to the bottled water is best expressed in terms of her arm length. Once she establishes that the water is reachable, she needs to pick up the bottle. Now Sue's arm length is not particularly helpful. Instead, her hand size is the relevant aspect of her body for the task, and her visual perceptual system expresses the size of the bottle as a proportion of hand size. In both cases, the visual system scales the environment to the relevant aspect of the body needed for action. What follows is a brief review of the literature supporting the claim that visual perception varies with changes in the body's morphology, physiological resources, and behavior.

PERCEPTION AS A PHENOTYPIC EXPRESSION

Morphology

Morphology consists of the body's semi-permanent form, composition, and size (Proffitt & Linkenauger, 2013). As previously discussed, the selected perceptual ruler depends on the aspect of the body relevant for acting; for example, when reaching for objects, arm length is the relevant structure of the body's morphology. In reaching, the action boundary is the point in space at which an object is just reachable and the space within the action boundary is defined as near space (Witt, Proffitt, & Epstein, 2005). Neural evidence demonstrates that the brain maps near space to include objects that are within arm's reach. Cognitive neuroscience provides compelling evidence for the psychological reality of the near space distinction as defined by the perceptual ruler, reachability. Patients with left visual neglect will ignore the left half of the visual field and exhibit a rightward bias when asked to bisect a line. Patients with left visual neglect only in near space will not exhibit a bias for lines outside of their reachability. However, these patients will show a rightward bias to far lines if their arms' reach is extended with a stick (Cowey, Small, & Ellis 1994; Halligan & Marshall, 1991), and recent fMRI research with healthy participants also indicates that the extending arm's reach remaps near space (Gallivan, Cavina-Pratesi, & Culham, 2009). Additionally, single-cell recordings in monkeys have found that neurons responding to objects within near space are also sensitive to reachability. Iriki, Tanaka, and Iwamura (1996) extended monkeys' reach with a rake and found that the visual neurons coding near space adjusted and responded to objects within the reach of the rake. From the above studies, it is evident that the visual system is sensitive to the body's reachability ruler.

Like the neural maps of near space, visual perception to objects within near space are also sensitive to arm's length and reachability. Although participants generally overestimate their reach ability (Fischer, 2005; Rochat & Wraga, 1997), they report that objects within this action boundary are perceived as closer than objects outside of the action boundary (Witt et al., 2005). If distance perceptions are scaled to arm length when reaching, then extending the reach of the arm via tool use gives the visual system a longer ruler to scale the distance to the object. For example, suppose Sue's bottled water is 12 inches away. If her ruler is also 12 inches long, the bottle of water is one ruler length away. If Sue measures the distance with a ruler that is 24 inches long, the water is now .5 ruler lengths away.

Fig. 3. The red target dot is the same distance away for both participants. Since the participant on the left has a shorter arm than the participant on the right, their ruler is compressed and the dot is perceived to be farther away.¹

Similarly, extending the length of the arm with a tool should result in a compression of distance for the now reachable objects (see Fig. 3 for an illustration of this principle). Indeed, research shows that when participants are allowed to reach with a tool, objects previously outside of arm's length but within the extended action boundary are perceived as closer than when reaching without the tool (Witt et al., 2005; Witt & Proffitt, 2008). This effect has been replicated with indirect measures of distance (Witt, 2011), and with remote tool use (Bloesch, Davoli, Roth, Brockmole, & Abrams, 2012). These studies clearly demonstrate that our visual perceptions of distance to objects in near space are scaled to the length of our reachability ruler.

Other aspects of the body's morphology also affect visual perception. In addition to the previously discussed eye-height and reaching studies, research shows that hand size influences the estimations of the weight and sizes of objects (Haggard & Jundi, 2009; Linkenauger, Mohler, & Proffitt, 2011; Linkenauger, Ramenzoni, & Proffitt, 2010; Linkenauger, Witt, & Proffitt, 2011), the ability to walk through a gap affects perceived size of doorways (Stefanucci & Geuss, 2009), the ability to jump across gaps alters the perceived size of the gap (Lessard, Linkenauger, & Proffitt, 2009), and altering the perceived body size in virtual reality changes the perceived size of the virtual reality world (van der Hoort, Guterstam, & Ehrsson, 2011). In a given situation, our visual perceptions are scaled to that aspect of the body that is relevant for acting in the environment.

Physiology

Imagine walking across a large, rolling field. In this environment, there are a number of candidates for scaling distance and slant perception. One could imagine the distance is represented in the number of steps required or even total travel time. Since all biological organisms must regulate their energy intake and consumption (Schrödinger, 1945), an especially useful perceptual ruler is the body's physiological costs associated with walking the extent. A review of the research indicates that for long distances and hill slants, visual perceptions are scaled to the amount of physiological energy required to traverse the extent

Fig. 4. Participants estimating the slant of a hill. *On the left:* The participant is using a palmboard to estimate an approximately 25 degree hill. Without looking at her hand, she adjusts the slant of the board to match the slant of the hill. *On the right:* The participant visually adjusts a disc so that the slope of the moveable piece matches the slope of the hill, which measures approximately 6 degrees.

relative to the amount of bioenergetic resources available (Proffitt, 2006; Proffitt & Linkenauger, 2013).

In general, the visual system overestimates the slants of hills (see Fig. 4). Participants standing at the bottom of a 10-degree hill estimate the slant to be approximately 30 degrees (Proffitt, Bhalla, Gossweiler, & Midgett, 1995). Furthermore, participants who are not physically fit, are physically fatigued, elderly, or weighed down with a heavy backpack report the slant of a hill to be steeper than their counterparts (Bhalla & Proffitt, 1999). These results indicate that participants also report hills to appear steeper when their energy potential is decreased.

Subsequent research suggests the perception of hill slant is directly linked to a physiological measure of energy, blood glucose. In one study, participants fasted prior to participation, and were assigned to either drink a sweetened or sugar-free drink. Following a depleting cognitive task, the participants who consumed the sugary drink reported the slant of a hill to be less steep than those who drank the sugar-free version (Schnall, Zadra, & Proffitt, 2010). In another study, participants gave slant estimates and then chose a drink to consume from a variety of beverages. The participants that gave steeper slant estimates were more likely to choose energy-replenishing drinks (Taylor-Covill & Eves, 2014). This research demonstrates that our perceptions of slant depend, in part, on the available physiological energy to act in the environment.

There are similar findings in the literature for distance perception. In virtual reality environments, experimenters can independently manipulate participants' walking speed and optic flow. When optic flow is set to be slower than the actual walking speed, participants implicitly learn that more walking effort is needed to travel in the environment (Anstis, 1995; Durgin & Pelah, 1999). In one study, researchers manipulated the optic flow of the virtual environment to be slower than the actual walking speed. Subsequently, these

participants estimated distances in the environment to appear farther (Proffitt, Stefanucci, Banton, & Epstein, 2003). Additionally, distance perception has also been directly linked to blood glucose. Cole and Balcetis (2013) had participants fast and then consume either a sweetened or sugar-free drink. Participants who drank the sugared drink reported distances to appear closer than those who drank the sugar-free version.

Research in individual differences in physical fitness provides the strongest evidence for the claim that distance perception is scaled to physiological energy. In one study, participants' maximal aerobic capacity (VO_2) max at blood lactate threshold, the gold-standard measure of physical fitness, predicted distance perception (Zadra, Schnall, Weltman, & Proffitt, 2010). Individuals higher in fitness perceived distances to be closer compared to individuals lower in physical fitness. Collectively, this body of work suggests that the visual perceptual system is sensitive to the physiological energy required to act in the environment. When the amount of available energy is low, the perceptual ruler is smaller, and so hills appear steeper and distances appear farther.

Behavior

Finally, an organism's purposes and goals also functions to influence visual perceptions. Goals influence what actions people intend to perform, and the selected action in turn determines what aspect of the body is relevant for use as a perceptual ruler. As discussed previously, when reaching for an object, arm length is relevant; when ducking under a branch, head height is relevant. Moreover, research demonstrates that the notion of relevance includes the intention to act. Objects within the reach of a tool do not appear closer if the participant is holding the tool, but does not intend to reach with it (Witt et al., 2005). Following an optic flow manipulation where participants have implicitly learned that it takes more energy to walk, distances do not appear closer if the participants intend to throw a beanbag to a target, rather than walk the distance (Witt, Proffitt, & Epstein, 2004). An individual's goals influence intended actions, which in turn determine what aspect of the phenotype is relevant for scaling visual perception.

In goal-directed behavior, performance predicts perception of target size. Softball players with a better batting average perceived a softball to appear larger (Witt & Proffitt, 2005), golfers who were better putters reported that the target hole appeared bigger (Witt, Linkenauger, Bakdash, & Proffitt, 2008), participants with better performance in throwing darts perceived the target to be larger (Cañal-Bruland & van der Kamp, 2009; Cañal-Bruland, Pijpers, & Oudejans, 2010; Wesp, Cichello, Gracia, & Davis, 2004), and field goal kickers with better performance perceived the distance between the goal posts to be larger (Witt & Dorsch, 2009). Here, the notion is that the relevant perceptual ruler is the variability distribution of performance around a particular target. When putting performance is good, the distribution of putts around the target hole is smaller, and so the target appears larger, and vice versa (see Fig. 5). For goal-directed behaviors, the relevant perceptual ruler is the variability in performance around the target.

Fig. 5. Each curve represents the variability of putting performance, which is the ruler by which the hole size can be scaled. *On the left*: For a putter with worse performance, the variability around the hole is larger, and so the hole is perceived to be smaller. *On the right*: For a putter with better performance, the variability around the hole is smaller, and so the hole is perceived to be larger.¹

THE SOCIO-ECOLOGICAL ENVIRONMENT AND PERCEPTION

For the remainder of the paper, we discuss how the socio-ecological environment functions within the framework of visual perception as a phenotypic expression. To provide a complete account of how the visual system functions, we must also consider how the body interacts with the surrounding social ecology. First, we propose that the social environment consists of available social resources, and we suggest that social resources function by extending or contracting the relevant physiological ruler. We then turn to research in smell perception to illustrate how ecology can determine what is relevant in perception. Finally, we highlight previous work on individual differences as an example of how to further research in the area.

Humans function as part of a larger ecological environment. Visual perception is scaled to the body's phenotype, but we must also consider how the phenotype is suited to our particular environment. Certain aspects of our ecology are common to all humans. Principles of evolution and natural selection dictate that our behavior rests on acquiring and husbanding energy resources and successfully reproducing. How these principles manifest in behavior varies with the ecology. Each individual lives in a unique environment that affords different action capabilities, has distinctive challenges to survival, and offers various opportunities for social interactions. A complete account of visual perception should thus also consider the socio-ecological environment and how it influences perception.

Social Resources

Humans are social animals that function as part of complex social environment. Our relationships with others offer valuable social resources. Like physical resources, social resources have also been shown to alter visual perception. Schnall and colleagues (Schnall, Harber, Stefanucci, & Proffitt, 2008) recruited participants either walking alone or walking with a friend and obtained visual estimates of slant. Participants walking with a friend estimated the hill to be less steep. Moreover, there was a significant positive relationship

between visual slant estimates and the length of the friends' relationship; the longer the friendship the less steep the perceptual estimates (Schnall et al., 2008). Participants who imagined a supportive friend also gave lower slant estimates (Schnall et al., 2008). This effect was replicated with another study where participants who browsed the Facebook profile of a supportive friend also gave lower slant estimates (Faulkner & Clore, 2012). Finally, in another study, researchers induced a sense of felt understanding or misunderstanding between participants. Those who felt understood by their fellow participants gave lower slant estimates (Oishi, Schiller, & Gross, 2012). The presence of or imagining a supportive other are indications of social resources, and our visual perceptions are influenced by these social resources.

Alternatively, social environments do not always indicate more available social resources. The presence of others may also signal a potential cost to the perceiver. Indeed, individuals perceive aggressive male students to be standing closer than non-aggressive male students (Cole, Balci, & Dunning, 2013), and threatening out-group members are perceived to be closer than non-threatening out group members (Xiao & van Bavel, 2012). Interestingly, recent work in visual perception suggests that highlighting the potential costs of cooperating on a task will negate the benefits of working together (Meagher & Marsh, 2014). In a series of studies, participants expected to carry a heavy box a target distance of 10 meters, and were assigned to either carry the box jointly with a confederate or alone. When the researchers made the difficulty of coordinating the task salient, participants in the joint-carrying condition estimated the distance to be farther (Meagher & Marsh, 2014). The nature of the social environment varies, and our perceptual system is sensitive to the fact that social networks can function both as an added benefit or an added cost.

However, it is not the case that the presence of a supportive or threatening others is considered a tangible resource or cost by which our perceptions are scaled. Instead, we hypothesize that our social networks afford opportunities for offloading work and acquiring more physiological resources. Through a process of load sharing (Coan, Brown, & Beckes, 2013), social resources are indications of more available cognitive and physical resources. This principle of load sharing is best illustrated with an example from behavioral ecology. When ostriches feed in groups, they divide the amount of food to consume among the group, and thus, there is less food available for each individual. However, because the group shares the responsibility of scanning for predators, each individual ostrich has more time to feed, and therefore, actually consumes more food than when feeding alone (Bertram, 1980). By offloading the cost of scanning for predators, the group affords the opportunity for each ostrich to consume more resources. For visual perception, the presence of others functions as a signal that more or less physiological resources are obtainable. The social environment alters visual perceptions by extending or contracting the relevant resource-specific perceptual ruler.

Ecology

The ecological environment also determines the relevant perceptual ruler. This is obvious when considering the surrounding physical environment. Stairs indicate that leg length is the appropriate visual perceptual ruler, and a door indicates shoulder width to be

the relevant aspect of our morphology. Taking inspiration from research in smell and attractiveness, we offer one final example of how social ecology shapes perception. In attractiveness, other individuals are the most attractive when they signal a strong likelihood of reproductive success. Humans maximize their chances at reproductive success by having offspring with robust immune systems. This goal can be accomplished by choosing mates with maximally different immune systems from their own. In this way, the ecological environment dictates that the immune system is relevant for attractiveness.

In humans, the genetic coding for the immune system is on the major histocompatibility complex (MHC), a small set of highly variable genes on a single chromosome (Wedekind, Seebeck, Bettens, & Paepke, 1995). Importantly, the MHC also determines each individual's unique body odor, meaning information regarding the composition of the immune system is readily available in body odor. This suggests that body odor can act as a reliable signal for immune system compatibility and, ultimately, signal reproductive fitness. Researchers have investigated this hypothesis in a study on body odor and attractiveness (Wedekind et al., 1995). In their study, Wedekind and colleagues investigated whether immune system compatibility affected perceptions of body odor. Male participants wore plain t-shirts for one week, after which the female participants smelled the t-shirts and rated each on pleasantness and attractiveness. The women gave the highest attractiveness ratings to the t-shirts worn by men with maximally different immune systems from their own. These results show that the information for attractiveness is the complement of our own immune system, which is an indication of reproductive compatibility. In this case of attractiveness, our human ecology selected the complement of our immune system to be the relevant ruler by which we scale our perceptions of attractiveness.

FUTURE DIRECTIONS AND CONCLUSION

In moving forward, we suggest that research in individual differences is a useful method to investigate how the socio-ecological environment is reflected in perception. Previous research on the effects of physiological and social resources on visual perception highlights the important contributions from studies in individual differences. As previously discussed, Zadra et al. (2010) found that individual differences in physical fitness, as measured by maximal aerobic capacity (VO₂ max) at blood lactate threshold, predicted distance estimations. The more physically fit the participants, the closer they perceived objects in the environment. This study is particularly valuable because it is a strong test of the hypothesis that visual perception is scaled to physiological resources. In this study, scores on the dependent measure were obtained prior to any experimental manipulation, and thus, cannot be attributed to demand characteristics or other confounding variables.

Additionally, individual differences in measures of extraversion interact with social support to predict slant perception (Gross & Proffitt, 2014). When participants imagined a supportive friend, extraversion was negatively related to slant perception; the more extraverted the individual, the lower the slant estimates. However, when participants wrote about a time when a friend had betrayed them, there was a significant positive relationship

between extraversion and slant estimates. In this condition, the more extraverted participants gave much steeper slant estimates. This study captures an important aspect of the social environment that would be undetectable with mean group differences. In investigating the effect of social resources in visual perception, stable personality traits interact with the social environment to produce drastically different effects. Investigations into individual differences go beyond yes/no answers and offer insight to the complex interactions between individuals and their socio-ecological environments.

In conclusion, a fundamental problem in the study of visual perception is the need to specify the metric employed to transform angular optical information into linear spatial units appropriate for specifying size and extents. An embodied approach to perception suggests that our phenotype provides the requisite perceptual rulers. Specifically, we discussed the evidence that our visual perception is scaled to the body's morphology, physiology, and behavior. However, this embodied account has not yet accounted for socio-ecological influences in visual perception. We argue that our social resources also affect perception, largely by increasing physiological resources through offloading work to the social network. Furthermore, we suggest that the ecological environment shapes perception by selecting the relevant aspect of the body to serve as a perceptual ruler. In moving forward, we suggest testing predictions with an individual differences approach. In sum, a complete account of visual perception necessarily includes not only the body, but also the socio-ecological environment in which the body functions.

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