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PERSPECTIVE

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Attention and platypuses

Sarah Shomstein | **Xiaoli Zhang** | **Dick Dubbelde**

Department of Psychological and Brain Sciences, George Washington University, Washington, District of Columbia, USA

Correspondence
Sarah Shomstein, Department of Psychological and Brain Sciences, George Washington University, Washington, DC, USA.
Email: shom@gwu.edu

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Abstract

This perspective piece discusses a set of attentional phenomena that are not easily accommodated within current theories of attentional selection. We call these phenomena attentional platypuses, as they allude to an observation that within biological taxonomies the platypus does not fit into either mammal or bird categories. Similarly, attentional phenomena that do not fit neatly within current attentional models suggest that current models are in need of a revision. We list a few instances of the "attentional platypuses" and then offer a new approach, that we term dynamically weighted prioritization, stipulating that multiple factors impinge onto the attentional priority map, each with a corresponding weight. The interaction between factors and their corresponding weights determines the current state of the priority map which subsequently constrains/guides attentional allocation. We propose that this new approach should be considered as a supplement to existing models of attention, especially those that emphasize categorical organizations.

This article is categorized under:

Psychology > Attention
Psychology > Perception and Psychophysics
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KEYWORDS

attentional selection, attentional weighting, dynamic prioritization

1 | INTRODUCTION

For this issue of WIREs we were invited to provide a perspective on "what is attention?" As researchers who study attention, our papers usually follow a similar script: give an example of a sensory overload, then appeal to the need to have a mechanism in place to sub-select some information from the overload for further processing, then define attention as selection. For example, in the most recent review from our lab (Shomstein et al., 2019) we start by posing the question of how does the human visual system sort through the massive amounts of sensory input, which it samples almost continuously, to arrive at a coherent perception of a scene? Then, we make the point that this process of searching through the environment for information is a ubiquitous component of sensory processing and it reflects a remarkable ability of the perceptual system to dynamically select information that is relevant for the current goal of the organism. Then, we finally get to the definition that the act of perceptual selectivity is what we call attention, and that this selection process is central to cognition. We could stop right here, since we defined attention as a selection mechanism, but this would hardly be satisfying to the reader, nor frankly to us.

Defining attention as a selection process is likely not going to stir much controversy, especially since this stems from William James' remark that attention is the "… taking possession by the mind, in clear and vivid form, of one out what seem several simultaneously possible objects or trains of thought" (James & Drummond, 1890). However, where things start to break down is when we try to further deconstruct what selection is. What is being selected? How is it selected? What does it mean for information to be selected?

As a scientific field we emphasize specificity and thus place value on putting forth testable models, and attention is no exception. Models of attention are many and focus on different aspects of the selection mechanism (similar to selection questions mentioned above). Some models focus on where the bottleneck of selection is, for example, early versus late and perceptual load theories of attention (Benoni & Tsal, 2013; Broadbent, 1958; Lavie et al., 2004; Makovski et al., 2014; Mevorach et al., 2014). Others focus on factors that guide selection, for example, top-down and bottom-up sources, and history (Awh et al., 2012; H. E. Egeth & Yantis, 1997; Itti & Koch, 2000). Yet, others focus on what it means for the signals in early sensory regions to instantiate selection, for example, divisive normalization (Denison et al., 2021; Li et al., 2015; Ni & Maunsell, 2017). This list of models is in no way meant to be exhaustive, but offers a small flavor of the kinds of aspects of attentional selection that are at the forefront of mechanistic investigations. Models are extremely helpful in helping fine tune our understanding of attention, and have been proven to be extremely fruitful in terms of driving inquiry. One concern with most of these models, however, is the issue of falsifiability. Few of these models clearly outline conditions under which the models will be clearly falsifiable, thus, when a new discovery or phenomenon pops up that does not easily fit into this or that theory, there is a tendency, for some, to raise a righteous finger and say "see, you have ill-defined theories of attention, and thus you do not even know what you are studying!" This is where we think it is important to remind ourselves that: (i) what we are doing is reverse engineering a system, the workings of which are currently at the level of hypotheses; (ii) outlining models is necessary in order to arrive at the ultimate 'correct answer' of how the system works; (iii) current models are just that – current – and are by definition flawed; and (iv) if a model is found to be insufficient, it is no reason to claim ignorance in what we are doing, rather, it is a reason to tweak the models and continue testing and improving them; and finally (v) at some point it might no longer be useful to hold on to a particular model as it might feel like trying to fit a square peg into a round hole. It is this last point that the title of our opinion piece is making a reference to—the attentional platypus.

2 | WHAT'S WITH THE PLATYPUS?

As an example, let us consider the top-down and bottom-up model of attention. Until relatively recently, reviewing decades of behavioral research led to a synthesis that the distribution of attention is largely guided by intentions of the observer (top-down) as well as by the salience of the physical stimulus (capture or bottom-up). A classic example of capture is a single raspberry in a bowl of blueberries, or the siren of a fire truck. In both cases, salience is defined by signals that are sufficiently different from the sensory environment they are embedded in by standing out from the context. On the flip side of capture, or bottom-up attention, is attentional guidance that is under full control of the organism. An example of such top-down attentional control is focusing on a particular aspect of a sensory environment. For example, when meeting a friend in a crowded square (before COVID), knowing that your friend is wearing a red t-shirt will guide your search to focus predominantly through people who are wearing red (H. E. Egeth & Yantis, 1997; J. M. Wolfe, 2021). This is an example of feature-based selection (Liu, 2019; Treisman & Gelade, 1980). Another type of top-down guidance is space-based selection: knowing that your friend is meeting you at the NW corner, you will directly attend that specific spatial location on the crowded square (Posner, 1980). More recently, a large body of attention phenomena have emerged that could not be easily accommodated into a top-down and bottom-up guidance network (Awh et al., 2012). These phenomena include things like guidance of attention based on various expectations either set by prior associated value, prior knowledge of spatial occurrence, or by various contingencies of the stimulus (Anderson et al., 2011; Drummond & Shomstein, 2010; Geng & Behrmann, 2002, 2005; Moore & Egeth, 1998; Shaw, 1978; Shomstein & Yantis, 2004). In response to the amassed volume of attentional platypuses (evidence), the traditional two-factor top-down and bottom-up attentional guidance theory was revised to accommodate a third factor—hysteresis. This revision was indeed a welcomed change as now a whole host of attentional phenomena have found their home in an attentional model, thus paving the way for new investigations of this tri-factor model of attentional control (Awh et al., 2012). This new approach ushered in a renewed interest into attentional selection, and the paper itself resonated with researchers, having been cited over 1300 times. Several follow-up review articles that further clarified the tri-factor model followed (e.g., see Theeuwes, 2018a) and a set of commentary papers that followed (Becker, 2018; Chelazzi & Santandrea, 2018; H. Egeth, 2018; Gaspelin & Luck, 2018; Kryklywy & Todd, 2018; Sisk et al., 2018; Theeuwes, 2018b; J. Wolfe, 2018).

We argue, however, that while this approach has been fruitful, it is still limited and it compresses disparate effects together for the sake of organizational clarity. This is akin to evolutionary taxonomy, and it is where taking a cue from the animal kingdom might be helpful. Traditionally, among the vertebrates, there are fish, amphibians, reptiles, birds, and of course the mammals. This is a compelling organizational structure, it explains most of the variance among the vertebrates that you will ever see, and for this reason it is still taught in elementary schools. Digging a bit deeper though, it begins to fall apart. Where are we to put platypuses with the fur of a mammal but the eggs and beak of a bird? Where do we put lungfishes with the body of a fish but the lungs of an amphibian? Quite a few attentional phenomena can be called attentional platypuses in their inability to fit neatly into the tri-factor model.

Recent research has shown several examples of potential attentional platypuses, attentional effects that do not seem to fit into any of the three traditional boxes of the tri-factor model: top-down, bottom-up, and hysteresis. These effects include most attentional phenomena associated with task-irrelevant sensory information impinging on attentional control (e.g., semantic relatedness, object size, spontaneous cognitive states, rhythmic fluctuations, strategies). These platypus effects are neither top-down or bottom-up, and they are not easily explained by hysteresis (without stretching the concept to an almost uncomfortable all-inclusive catchall third box), but they nevertheless exert influence on attentional orienting. For example, the influence of task-irrelevant items on attentional orienting could be argued to be top-down, as the target location can be defined by its spatial relationships to the nontargets, but this could also be argued as hysteresis, as these relationships are only known after seeing the spatial structure of the trial. If task-irrelevant influences on attention are mammals, and hysteresis effects are birds, then this effect of non-targets is certainly a platypus.

In the next few sections, we will exemplify a few instances of attentional effects that fit poorly (attentional platypuses, see Figure 1) into the tri-factor model of attention, and then suggest a possible way forward, the dynamically weighted prioritization approach, that is more flexible in terms of accommodating attentional platypuses. While we do not argue against the tri-factor model, and appreciate the benefit of organizing attentional selection in these terms, we submit that a more detailed model of attentional taxonomy could liberate us, as a field, to yield new investigations and lead to new models.

3 | EXAMPLES OF SOME PLATYPUSES

3.1 | Task-irrelevant object size

Size is an intrinsic attribute of all objects in the physical world, and its computation is inherently present given the retinotopic nature of visual processing in the ventral visual system (i.e., size of the retinal image and observer's distance) (Baird, 1963; Hubbard et al., 1989). Castiello and Umiltà (1990) demonstrated that if participants were asked to respond to a presence of a target, their response times were modulated by the size of the box in which the target was embedded. In a more recent experiment, Nah et al. (2018) demonstrated that size can also affect attentional shifting. Using an adapted Egly paradigm (Egly et al., 1994) in which the classic rectangles were replaced by trapezoids, attentional shifting was slower when shifting to the thin end of a trapezoid than when shifting to the thick end. The authors argue that this is a manifestation of Fitt's law, the phenomenon known from the motor system in which larger objects

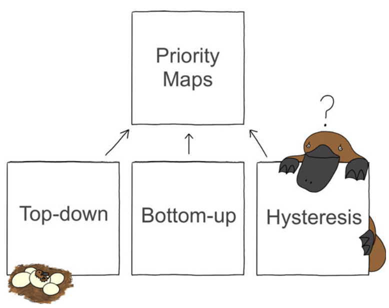

FIGURE 1 A graphical representation of a tri-factor model of attention, modified to include an attentional platypus—an attentional factor that guides attention but does not easily fit into either one of the three boxes

are more quickly acted upon than smaller objects (Fitts, 1954). Both studies demonstrate that size is an inherent property of an object and that it has ramifications on the functioning of attention. In either of these cases, size of the object was irrelevant to the task at hand, neither was it a salient feature, nor was there a particular history associated with any of the objects that is unique under large or small instances. As such, task-irrelevant size of the object, and its influence on attentional allocation, is not easily accommodated by current theories of attentional control.

Furthermore, Collegio et al. (2019) demonstrated that semantically known size, rather than retinal size, impacts attentional allocation. In their paradigm, a line drawing of a known object, such as a domino or a kayak, was presented at a fixed retinal size at fixation. One end of the object was then cued and a target appeared either at the cued end of the object, or on the other side of the object. It was found that participants were slower to respond to the invalid target when the object was known to be large (e.g., kayak) than when it was known to be small (e.g., domino). The influence of the inferred object size was observed despite the exact same retinal size in which all objects were presented.

In both instances of object size influencing attentional allocation (physical size differences and object semantic size), size was a task-irrelevant factor that influenced attentional allocation and is a factor that is not easily accommodated by a tri-factor model.

3.2 | Task-irrelevant semantic relationships

In recent years there has been a renewed interest in findings showing that semantic and category information is rapidly processed (Biederman et al., 1974; Greene & Oliva, 2009; Potter, 1975) in a manner that minimally engages attentional selection. Several studies extended this observation to suggest that semantic and category information of items maintained in working memory tend to influence attentional allocation. For instance, a search target (e.g., a chimney) stored in visual working memory (VWM) facilitates the directing of attention toward likely positions in a scene (a roof) with the very first eye movement (Castelhano & Heaven, 2010; Eckstein et al., 2006; Malcolm & Henderson, 2010; Neider & Zelinsky, 2006). Similarly, an object stored in VWM (e.g., a motorcycle) increases the likelihood that a viewer will attend to semantically related objects (a motorcycle helmet) (Belke et al., 2008; Hwang et al., 2011; Mack & Eckstein, 2011; Moores et al., 2003), or that semantically related distractors will capture attention (Belke et al., 2008; Moores et al., 2003).

In the cases described above where task-relevant semantic and category information guides attentional selection, these guiding factors can be easily placed into the hysteresis box of the tri-factor model of attention. However, the attentional platypus appears when semantic/category factors become irrelevant to the task as it no longer fits into top-down or hysteresis, and it is not capture. In a recent study, Malcolm et al., 2016, showed that when presented with task-irrelevant objects, the object semantic relatedness influences attention even if object identity and semantic relationships are not predictive of the task at hand. In a set of follow-up functional magnetic resonance imaging (fMRI) experiments, Nah et al. (2021) fleshed out the neural network that is responsible for task-irrelevant semantic influence on attentional selection. It was shown that the left inferior frontal gyrus (IFG) shows sensitivity to object semantic relatedness, with activity in IFG directly predicting the degree of behavioral benefit of faster response times for targets that appear on task-irrelevant semantically related objects. It was also shown that semantic relatedness then likely biases spatial attention maps in the intraparietal sulcus, subsequently modulating early visual cortex activity. These results suggested that if an object is attended, its semantic properties bias attention, even if it is irrelevant to the ongoing task or if more predictive factors are available, outlining a factor of attentional selection not easily accommodated by prior models of attentional selection.

Taken together, our results, and those of others, show that the semantic content and the relative semantic relationships, even while task irrelevant, exert their influence on attentional allocation and is a factor that is not easily accommodated by a tri-factor model.

3.3 | Spontaneous cognitive states

Along the lines of attention research focusing on external factors (such as physical salience, task goals from explicit instruction, the in-flowing experience during the experimental session, as well as task-irrelevant size and semantics discussed in previous sections), there have been other lines of research looking at the degree to which internal factors, such as spontaneous cognitive states, influence attention. The latter cannot be intuitively categorized as bottom-up, top-down, or history-driven processing. Although these spontaneous factors have not been included in the tri-factor model of attention, there is considerable evidence in the literature that these seemingly task-irrelevant factors nonetheless play a role during attention deployment.

Several recent theories argue that cognitive states influence attention and perception (Goldstone et al., 2015; Lupyan, 2017; although there is ongoing debate about whether cognitive states actually influence judgments or responses instead of perception per se, Firestone & Scholl, 2016). For example, knowledge can greatly influence the perception of bistable or ambiguous images (Meng & Tong, 2004; Tong et al., 1998). Attention is also known to be biased toward emotional materials, interacting with the emotional states of the individuals (see a review in Yiend, 2010). For example, patients with generalized anxiety disorder (GAD) experienced more interference on a cognitive task from threat words occurring in the unattended auditory channel, compared to control participants (Mathews & MacLeod, 1986). This finding suggests that patients with GAD may prioritize threat words differently from control participants. While emotional *stimuli* can be attributed to hysteresis defined as a broader term (e.g., “previous experience” instead of narrowly “past selection history” as defined in Awh et al., 2012), the emotional *state* of the observer cannot easily be accommodated. Similarly, intention or voluntary action is another internal factor that can guide our attention allocation, separate from top-down attention modulated by task goals. For example, participants could voluntarily shift attention between two locations and these voluntary, not-task restricted shifts of attentional focus have been successfully tracked by neural activities in the brain (Gmeindl et al., 2016). Furthermore, attention to intention has been found to have neural substrates in prefrontal and presupplementary motor areas (Lau et al., 2004), indicating the biological possibility for the influence of internal intention on attention.

These spontaneous processes of knowledge, emotions, intention, and others are typically not explicitly instructed and can be considered as task-irrelevant within current attentional models. Their influences on attentional selection are supported by growing evidence, but may have been inadvertently left out of the more traditional definitions of attention.

3.4 | Rhythmic fluctuations

There is an important assumption that is often made in many attention studies, as well as in the tri-factor model: that the attentional states are stable throughout the course of the experiment session. This simplification on the one hand helps with noise reduction and theoretical interpretation of the results, but on the other hand hides the dynamic nature of the attentional processes. If we look specifically at the temporal dimension, we can find rhythmic oscillations in attentional performance. For example, with explicit instruction to sustain attention at one location, participants show lapses in their responses in rhythmic patterns (Smith et al., 2003), which may indicate fluctuations of attentional prioritization. These behavioral patterns may be tied with intrinsic neural rhythms in the brain, especially those in attention-related regions (Fiebelkorn & Kastner, 2019) and activities in the default-mode network (Sali et al., 2016). This spontaneous fluctuation of attention is sometimes explained by one common and long-studied phenomenon called inhibition of return (IOR)—the tendency that spatial attention is inhibited to orient to the previously attended location (Posner et al., 1985). However, the studies of the IOR phenomenon itself do not often discuss it in the context of temporal attention on an elongated scale, and the temporal characteristics are rarely highlighted while discussing the definitions and models of attention. We propose that comprehensive understanding would require further exploration of these aspects as well.

3.5 | Strategies

Strategy is another higher-level cognition that has been proposed as playing a role in attentional selection. With the same instruction, participants may come up with different strategies to accomplish the task, which differs where and how their attention is allocated. For example, in a visual search paradigm where the optimal strategy is to change the color to search from trial to trial, participants tend to be sluggish to update the optimal color and there are substantial individual differences in using this optimal strategy (Irons & Leber, 2016). In some circumstances, participants' strategies may not even align with the task requirements. It has been found that attention sometimes may be geared toward objects or space which is neither beneficial to the current task goal nor of immediate perceptual priority, for example, toward novel stimuli (Becker & Horstmann, 2011; Ernst et al., 2020; Retell et al., 2016). Some researchers propose this behavior pattern as a spontaneous act for novelty seeking, which is important for exploration (Kakade & Dayan, 2002).

A relevant behavioral pattern comes from the load theory of attention: when perceptual load is low, participants pay more attention to the distractors, compared to the high perceptual load condition where perceptual capacity is exhausted on task-relevant stimuli (Lavie et al., 2004; a more recent review in Murphy et al., 2016). This may indicate a hardwired mechanism that makes it difficult to avoid attending to task-irrelevant stimuli in order to fill up perceptual capacity. Higher-level strategy or hardwired cognition is another factor that cannot be easily categorized in the tri-factor model of attention and our understanding of these mechanisms benefits little from simply categorizing them without studying their interactions with other attentional factors.

4 | WHAT DO WE LEARN FROM THE PLATYPUSES?

Studying attention is not too different from studying evolution. The way we learn about the evolution of life is not just by studying a single model organism in isolation, but rather by taking a wider view and observing the commonalities in the development of many different organisms. Similarly, while it was extremely useful to focus on developing general attentional models, an understanding of attention as a larger process requires sensitivity to the full range of factors (including the platypuses) that ultimately influence attentional allocation. The focus should now shift to not only delineating *which* factors influence attention, but examining similarities and differences between them, and, perhaps most importantly, on understanding *how* they interact.

Attentional research has amassed an incredible amount of knowledge regarding the general ways in which attention is allocated as well as the various factors that influence attention. We propose that the time is ripe to consider attentional allocation as a state in the dynamic priority map (Figure 2) which takes as input various factors that are known to influence attentional allocation (Bisley & Goldberg, 2010; Koch & Ullman, 1987; also see reviews Ptak, 2012; Shomstein & Gottlieb, 2016; Todd & Manaligod, 2018). The state dynamically changes as a function of multiple attentional factors that influence it, with corresponding weights that determine the degree of influence for that particular factor. This approach enables researchers to launch inquiries about the interactions between and among factors that influence attentional allocation. An added benefit of this approach is that no sensory stimulus is thought of in binary terms as task-irrelevant or not salient, rather, all sensory stimuli are contributing to attention and thus lack the need for a particular binary label or belonging status.

The current state of the priority map is likened to a Bayesian framework (Feldman & Friston, 2010; Friston, 2009) in which prior and current information about a particular attentional factor's reliability modulates the weight of that factor as a

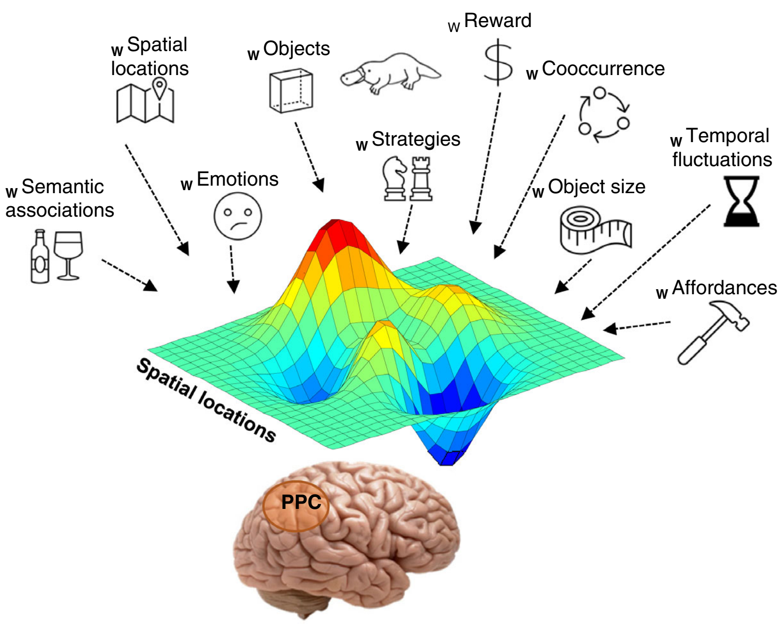

FIGURE 2 A representation of a dynamic state of the attentional priority map in the posterior parietal cortex (PPC). There are many factors that impinge on to the map and each has a weight associated with it. The weight is constrained by external factors (task, salience, etc.) as well as internal factors (prior experience, current fluctuation in the system, etc.)

constraint on the attentional priority map in posterior parietal cortex (Figure 2). Representations with a high weighting successfully contribute more to constraining attention, and factors with less weight contribute less. The weighting changes dynamically reflecting the current state of the system. As the weightings of some representations are reduced due to an increase in spatial uncertainty (e.g., you are less sure about where the target is), for example, other representations (e.g., objects) contribute to a greater extent, and therefore constrain attentional selection (Donovan et al., 2017; Drummond & Shomstein, 2013). We call this the Dynamic Prioritization Approach to predicting attentional allocation. Of course, we are perfectly aware that what we are arguing for here is ultimately a proposition to "study everything at once" and understand the challenge that is associated with it. However, more and more empirical evidence has accumulated showing that there is no such thing as an irrelevant sensory stimulus (see Shomstein et al., 2019 for most recent review). Perhaps one practical step in the process is to continue investigating the relative contribution of two attentional factors at once and their interactions (e.g., spatial locations and objects; objects and reward; certainty and emotion) and move on to multiple-way interactions. At the same time, investigating the profile of a complex and dynamic system from a zoom-out perspective can provide additional helpful insights.

Moreover, this dynamically weighted prioritization approach lends itself nicely to a somewhat neglected investigation of individual differences in attentional orienting. In a similar set of circumstances, attentional allocation (e.g., the state of the priority map) in two individuals might be different because of different weights associated with some or all of the attentional factors. This approach allows for not only studying what is similar among individuals (i.e., what factors are involved) but also how the relative contribution of each factor is determined through differential weighting according to individual differences.

We should note that the dynamically weighted prioritization approach that we put forward here suffers from a similar problem as other models of attention do—it is unclear whether it presents a clear case for falsifiability. Currently, our lab is on a mission to create a set of hypotheses that follow directly from this approach to test several boundary conditions that will ultimately help with figuring out conditions of falsifiability.

5 | CONCLUSION

In a way, the platypus metaphor is not a metaphor at all. The systems we are studying evolved in the exact same manner as platypuses (Cisek, 2019). If platypuses do not fall into neat boxes with birds or mammals, analogously there is no reason why factors that influence attention (those listed in Figure 2, for example) should either. When attentional platypuses are encountered in the "wild" we should not be trying to force them into groups with the birds or the mammals, but rather re-evaluate taxonomies. Going forward, we suggest that we think more in terms of continuities and dynamics. In essence, we should not force an arbitrary organization on the menagerie of attentional mechanisms which we have, but rather we should use the organization endemic to the system itself, prioritization.

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AUTHOR CONTRIBUTIONS

Sarah Shomstein: Conceptualization (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Xiaoli Zhang:** Conceptualization (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Dick Dubbelde:** Conceptualization (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Sarah Shomstein https://orcid.org/0000-0001-8278-6630
Xiaoli Zhang https://orcid.org/0000-0002-5608-9564

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