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Reply to comment

Situating and extending the sense of should
Reply to comments on “The sense of should: A biologically-based framework for modeling social pressure”

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We would like to thank Constant, Friston, and Ramstead [1], Fotopoulou [2], Jебari [3], Rai [4], Tsakiris [5], and Tummolini and Pezzulo [6] for their insightful comments. We are honored to have our work read so thoughtfully and by the encouragement to extend our thinking even further. Two themes we observe in the comments are (a) the question of what the boundaries of the sense of should are (including whether it has explanatory value in itself, or whether it is something to be explained), and (b) how it can be generative for understanding other social phenomena, such as politics, morality, and embodiment. We believe that these two themes complement each other, and that by clearly delineating the boundaries of the sense of should we can sharpen its theoretical connections to social cognition as understood in the broadest sense.

Constant et al. [1] draw attention to the central matter of whether the sense of should is an explanation of conformity in itself (i.e. an explanandum) or whether it is explained by more fundamental properties of metabolic efficiency implemented in a predictive brain (i.e. an explanans). In their view, “given the machinery of predictive processing, the sense of should—or any psychological trait—is something one gets ‘for free,’ in social systems”. We agree completely: our original intention was to suggest that the sense of should might emerge across development from the relationship between a social environment, metabolic efficiency, and predictive processing (see section 3.3 of the target paper [7]). In our view, the sense of should is not a psychological adaptation and is not selected for. What is selected for are the neurobiological changes that facilitate predictions and associations at high levels of abstraction (e.g. potentially, an expansion of neuropil in human prefrontal and association cortex, compared to chimpanzees [8]). We hypothesize that these domain-general changes in high-level brain structure may help humans learn complex contingencies, including those that link “your” expectations about “my” behavior to the social-environmental disruptions that follow when “your” expectations are violated.

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However, we also believe the sense of should can be useful as an explan 
in itself, depending on the scientific question and analytic approach (see Beni [9], to whom we owe thanks for his detailed discussion of this point). We hypothesize that the sense of should is an emergent product of predictive and metabolic machinery, but once it is conceptualized as a set of normative obligations it may have properties that are not easily reducible to these parts. Concepts, here, refer to learned sets of predictions acquired through cultural or personal experience [10,11]. In the target paper [7, p. 13], we quote Kohlberg’s description of two children feeling anticipatory anxiety (i.e. the sense of should) at the thought of stealing, where one interprets the feeling as “being chicken” and the other as “a conscience”—two concepts with drastically different behavioral implications. In our view, the sense of should is a crucial ingredient for normative concepts; but once norms are conceptualized, all bets are off, and behavior can no longer be reduced to its simplest ingredients. In this way, the sense of should could be a crucial explan when working at the psychological level—it provides motivational fuel, distinct from reputational concern, that feeds into normative concepts. Nonetheless, we agree that the more expansive free energy accounts and the more restrictive sense of should each complement the other [1,9].

Both Fotopoulou [2] and Rai [4] encourage us to be more ambitious in our scope, suggesting that we “focus on the costs of bodily rather than just brain metabolism” [2], or “do away with [our] distinctions between the social and the moral and the reputational and instead opt to explain all of it” [4]. We appreciate the encouragement, but we also want to carefully delineate what questions fall within the intended scope of the target paper, and what questions we see as belonging to more expansive accounts (e.g. of morality, and of embodied motivation in general). As one source of motivation the sense of should could have a lot of explanatory power, but its phenomenology and hypothesized function also impose constraints: the sense of should necessarily involves the motivational force of others’ expectations and the affective experience of anticipatory arousal.

Rai observes that the sense of should could set a strong foundation to explain non-WEIRD morality [12], where “much of morality is conformity” [4]. In particular, Rai notes that “internalized moral values”, which elicit the sense of should regardless of others’ expectations, are more often found in WEIRD cultures. Given this, Rai suggests that the distinction we set up between social and moral obligation may be best abandoned ([7], Fig 1). We think that the distinction matters, if only to keep the explanatory scope of the target paper clear. Even if only in WEIRD cultures (and for the specific sense of “moral” we have in mind, we think in non-WEIRD cultures also), people sometimes feel obligated to make things difficult for themselves by holding fast to their values against the expectations of others. And even if people who truly follow through on these commitments are rare, such martyrs are nonetheless held up as mythological exemplars. When and why such moral commitment occurs is beyond the scope of the target paper, but one hypothesis, which we plan to develop further [13], is that internalized moral values are patterns of behavior entrained by the sense of should which cannot be easily unlearned in a new social context. When you encounter a new culture, you will encounter some expectations that you are happy to conform to (i.e. conventions), but there may be others that violate your “moral principles”—i.e. expectations that you will continue to resist even when your resistance contributes to social uncertainty. From this perspective, there is no clear line separating moral and conventional norms [14,15], but moral norms may occupy a more central position in your predictive model of the social world (i.e. a central position in a Quinian web [16]). Abandoning these core moral values to potentially buy a little social predictability may do you more harm than good, as it would undermine foundational predictions about social behavior that structure your predictive model of the world. This is especially true given that humans are fundamentally social animals, where our biology, development, and metabolic health are all premised on group-living (a point nicely made in the comment by Fotopoulou [2]). We agree with Rai that a theory of morality/normativity should be grounded in factors that explain behavior in non-WEIRD cultures, but we also want to leave ourselves room to explain how psychological processes emphasized in WEIRD cultures could still emerge from the same underlying principles.

Fotopoulou outlines how our account of the sense of should could be connected to a radically embodied and developmental account of social cognition. Socially enculturated practices, beginning in infancy, allostatically optimize a range of metabolic variables. She suggests that people conform to cultural practices to optimize metabolic efficiency—and critically, metabolic efficiency considered in terms of the whole organism, rather than only the brain-based metabolic costs of prediction error that we considered. We completely support the project of developing a radically embodied account of value, motivation, and decision-making, and we agree that sociocultural practices should be considered in terms of their metabolic payoff, but we also think that the sense of should is better placed as subordinate (i.e. an explanandum) to a more general account of embodied motivation. For example, to explain why Amelia chooses to eat with Bob instead of painting her nails would require a more expansive account of motivation,
as opposed to just an account of social pressure via the *sense of should*. In our paper we focused on the metabolic underpinning of the *sense of should* because it was an oft-overlooked motivational source and a relatively more tractable problem. Much remains unknown about the complex interactions between metabolism in the brain and body, but the simpler link between information processing (i.e. prediction error) and brain metabolism can be more easily established by existing work, and can be more easily tied to phenomenology. For example, the involvement of anticipatory arousal in the *sense of should* may provide clues about its connection to neurochemistry and brain metabolism (see our response to Jebari below [3]). Nonetheless, Fotopoulou is correct that the actual role of metabolism and embodiment in motivation will almost certainly be more complex than we have outlined here. For now, we are content to highlight this particular link between brain and body, and we hope that future work can elaborate on it.

Fotopoulou also rightfully observes that humans are interdependent [17,18], rather than *a priori* ‘separated’ as our account assumes. We completely agree [19], but we set up the logic of our paper to show how the interdependence that the *sense of should* entails could come about even with the strong initial assumption that humans are perfectly independent, common in evolutionary psychology and game theoretic approaches (e.g. [20]). Relaxing this assumption of independence would allow for fruitful elaborations on the core principles we have tried to describe. Social interdependence can also emerge through other pathways, including through social affordances that others have integrated into predictive frameworks [21,22]. These affordances fall under the umbrella of *informational influence* as delineated in the target paper ([7], Fig. 1), and some of the cultural practices described by Fotopoulou may fall under this domain as well (e.g. entraining infants to eat at particular times). But what must be emphasized is that the *sense of should*, as we conceive of it, remains subordinate to more general accounts of embodied motivation, and not the other way around. Contextualizing the *sense of should* within a more general framework of embodied psychology would be extremely useful, but, for many purposes, we believe the current account can provide some novel insight on its own.

Rai [4] worried that our account may be unfalsifiable, but Jebari [3] points to a component of our formalization that would undermine the entire project if it could not be supported with additional empirical evidence. We are grateful for this criticism, as we believe it validates the theoretical strength of grounding our analysis in biology, where empirical findings will either support or disprove the assumptions we made. Our formalism implies that organisms should be able to differentiate between at least two sources of metabolic cost: metabolic costs of prediction error ($M_{pe}$) and metabolic costs of everything else ($M_e$). Because we characterize the *sense of should* as a distinctly felt motivation, linked to epistemic costs (measured by $M_{pe}$), our separation of epistemic (e.g. the *sense of should*) from pragmatic motivation (e.g. reputation) would not be tenable unless $M_{pe}$ was somehow separable from other metabolic costs. Although it was only briefly mentioned in the target article, an increasingly large body of work has outlined the physiological consequences of prediction error, in particular, its effects on autonomic arousal [23–31]. Of note, prediction error is associated with norepinephrine release, which itself intensifies the BOLD signal at sites of activation [28,32]. Other work has shown that norepinephrine also increases the consumption of glucose during sensory stimulation and cognitive activity [33]. This consumption of glucose proceeds by an alternative and more expensive pathway compared to the typical and more metabolically efficient oxidative pathway used by muscles and the resting brain. This alternative pathway is *aerobic glycolysis*, where *glycolysis*, the initial step of cellular respiration, inefficiently consumes glucose to generate ATP, extruding lactate as a waste produce. It is called *aerobic glycolysis* because *glycolysis* is used to generate ATP even though the $O_2$ needed to metabolize lactate is plentiful [34,35]—i.e. *aerobic glycolysis* means *glycolysis* in an *aerobic* environment. This use of *aerobic glycolysis* increases localized glucose consumption by $\sim 1500\%$ to generate the same net yield of ATP, meaning that although the net contribution of *aerobic glycolysis* to the energy yield is small, its metabolic footprint is massive in terms of the glucose consumed. The costs of prediction error ($M_{pe}$), then, may be separable from all other costs ($M_e$) by both the rate of glucose consumption and the involvement of norepinephrine. Outlining the full details and implications of this work would bring us beyond the scope of this response, but in our future work we plan to elaborate on the relationship between *aerobic glycolysis*, the BOLD signal, and prediction error [36]. In this way, the metabolic underpinnings of the *sense of should* can be more concretely formulated in terms of raw metabolites [37], as opposed to simple net ATP costs as they were initially cast in the target paper.

Tummolini and Pezzulo [6] redescribe our core distinction between the *sense of should* and reputational concern as a difference between epistemic and pragmatic value. We agree, and owe them a debt of gratitude for putting our account so succinctly. Tummolini and Pezzulo also suggest that the *sense of should* could be deconditioned by repeatedly violating others’ expectations (e.g. consistently passing cars from the outside and learning how people react). That is, through repeatedly violating norms, one may extinguish the anticipatory anxiety that contributes to the
sense of should in these contexts. Again, we completely agree, and recent empirical evidence supports this hypothesis [38]. But this point also highlights—somewhat shockingly—that the foundation of our social stability may be built on thin ice: the motivational glue keeping social structures together is only a subtle affective nudge toward not exploring the consequences of particular norm-violating actions, and it can be overcome with practice. From this perspective, regimes of physical or reputational punishment may be less the core force shaping social organization [39,40], and more a tool of last resort.

Another example of the deconditioning that Tummolini and Pezzulo describe may be the military training necessary to commit violence, where the percentage of United States soldiers voluntarily firing guns was increased after the Korean War by training soldiers in contexts that more accurately mirrored conditions on the battlefield [41, Chapter 2], [42]. Importantly, to overcome the sense of should, we predict that it is likely not enough to explicitly know or articulate the predictable consequences of an action. The learned aversion toward violating others’ expectations is associative, meaning that the predictions we are referring to include detailed trajectories of incoming sensory signals at all levels of abstraction (down to tastes, smells, sights, etc.), and the motor commands you should prepare in response. So, for example, although Jebari [3] suggests that after destroying a friend’s apartment “it is easy to predict that this would destroy our friendship, ruin my reputation, and undermine my housing situation (all of which plausibly increases [metabolic costs generically])”, we hypothesize that abstract predictions like these may do little to overcome the sense of should, as you still lack experience to inform specific and embodied predictions. Likewise, performing simple motor actions involved in violent acts triggers an arousal response, even when you know that no harm will come of it [43]. In line with Tummolini and Pezzulo, our framework predicts that the anticipatory anxiety felt when mimicking violent actions (or when actually trashing your friend’s apartment) will decrease with practice. The consequences (or lack of consequences) will also be learned, but we hypothesize that knowing something is “a bad idea” is a phenomenologically distinct motivation from the anxiety instilled by the sense of should. That is, with practice, one could decide against killing, but not feel anxiety about pulling the trigger.

Tsakiris [5] asks how the sense of should might interact with an embodied account of visceral politics, where politics is understood as the context and concepts that help us interpret our visceral experience and organize a society to meet our embodied needs. He asks how it could be considered adaptive for citizens to adopt concepts provided by figures like Donald Trump, which have led Americans to feel anxious, divided, and angry at their fellow citizens. Here, we reiterate that it is critical to separate the sense of should from its extensions. Our account of the sense of should is value-neutral, and simply articulates that short-term social predictability can be gained by adjusting oneself to fit others’ expectations. Broader trends and trajectories in politics, culture, and economics can mean that this conformity—performed collectively, but undertaken by each individual to satisfy her own short-term affective and metabolic needs—can doom us all over the long term (consider, for example, the current collective inaction on climate change). We should also note that the forms of political organization that the sense of should could facilitate may look morally repugnant from a contemporary perspective—but nonetheless, the motivation to conform that the sense of should instills would sustain the status quo, regardless of its content. For example, Tsakiris quotes Aristotle, who claims that “individuals cannot perform their natural functions apart from the city-state, since they are not self-sufficient”.1 But Aristotle also goes on to argue for the existence of natural slaves [45], where “people whose task, that is to say, the best thing to come from them, is to use their bodies are in this condition—those people are natural slaves. And it is better for them to be subject to this rule, since it is also better for [humans to rule animals, and men to rule women]” [46, pp. 8–9]. Our point is that many forms of social organization are possible—from the most egalitarian communes to the most despotic hierarchies—but in every case we suspect that the social structure is maintained by mutual webs of expectation. These expectations need not be symmetrical (and are clearly not between masters and slaves), but even in a society that aims for egalitarianism there may be a need for leadership, as the dynamics of the sense of should imply that leaders can act as a focal point to make expectations clear, coordinating the behavior of the

1 Aristotle remarks that human beings must necessarily be organized into a city-state, but it is worth noting that recent anthropological evidence has been interpreted to suggest that life in agrarian states may have harmed the health of individuals [44], decreasing food diversity and increasing disease and early mortality compared to contemporaneous hunter-gatherers (a.k.a. “barbarians”, from the perspective of the city-states). In a purely evolutionary sense, however, city-states may outcompete nomadic populations by decreasing the spacing between infant births, creating a cumulative advantage in population size over time [44, pp. 113–115]. It is critical then, to reiterate that metabolic health and reproductive rate are joint selective pressures. We have emphasized metabolic health in our work, but its connection to the broader evolutionary dynamics is of critical importance when the scope of investigation is widened.
group in ambiguous or novel situations. Given this, we predict that political structures are sustained when expectations and social roles are made clear to group members, and erode when they are not. In the current pandemic the absence of clear guidelines from American authorities at all levels of government may be contributing to a natural test of this hypothesis.

Finally, Rai worries that our account does not produce generative hypotheses [4]. While we strongly believe that there is utility in integrating, under one framework, existing work that was not previously reconcilable, we also believe that the strongest generative hypotheses from our account will stem from its embodied and material (i.e. metabolic) foundations that Fotopoulou [2] and Tsakiris [5] drew attention to. In particular, we believe our account may provide an alternative explanation for ingroup favoritism and outgroup derogation, a foundational topic in social psychology [47–49]. Traditional evolutionary accounts have hypothesized that human prosociality is inextricably tied to “tribalism”, with the implication that racism and sectarianism are tragic but inevitable byproducts of the evolutionary path that made human prosociality possible [50–52]. “Insofar as morality is a biological adaptation, it evolved not only as a device for putting Us ahead of Me, but as a device for putting Us ahead of Them” [50, p. 24]. As said above, our account is not an adaptationist one, and by explicitly connecting motivation to material resources, our account suggests an alternative: that metabolic factors may explain whether people prefer ingroup members or exclude out-group members. Ingroup members are familiar people who we share characteristics with, and outgroup members are unfamiliar people who differ from us. To control the social environment by the sense of should, one must infer other’s expectations. Inferring the expectations of familiar ingroup members necessarily requires less exploration and metabolic expenditure. Inferring the expectations of unfamiliar outgroup members necessarily requires more trial-and-error exploration before one can use conformity to facilitate a fluent and metabolically efficient social interaction [53]. Recent work demonstrates that people find it rewarding to have expectations (even stereotypes) confirmed [54], and general preferences for pattern consistency predict stigmatizing and prejudiced judgments [55]. We hypothesize that under conditions of metabolic scarcity, individuals will prefer to associate with familiar others; that is, instead of investing in the costly process of learning about outgroup members, they will prefer to avoid, ostracize, or otherwise remove outgroup members from their environment. Critically, by removing outgroup members they achieve the same metabolic end that the sense of should is hypothesized to promote: they make the social environment predictable—but by excluding unpredictable people rather than regulating them. These predictions are difficult to test in a laboratory environment, but we consider this a strength and not a weakness. Rather than operating on a lab-convenient operationalization (e.g. minimal groups paradigms; [56,57]), the hypotheses may be best tested in naturalistic conditions. For example, the anxious discomfort felt when talking to someone who is not fluent in the language they are trying to speak, or who has a heavy accent [58,59] may be a useful operationalization of the phenomenon we are trying to describe. Although it remains to be tested, our account suggests that sectarianism is a metabolic strategy, not the unfortunate and inevitable consequence of an evolutionarily inherited coalitional psychology [cf. [60,61]]. We hypothesize that this strategy can be made unattractive like any other, by changing both material conditions and the collective expectations of a community.

In sum, there are many ways of organizing ourselves collectively that are compatible with the sense of should felt by individuals. Constructing a better model to coordinate with unfamiliar outgroup members is one strategy, and another is to avoid and exclude them to metabolically coast on ingroup expectations that are already known. Perhaps the most important boundary to draw around the sense of should is that it may motivate normativity, but it is still something distinct from our moral concepts—i.e. our concepts of what a just world should be, inherited through a cultural and philosophical dialogue that has continued across history. From the perspective of how individuals manage the metabolic costs of their social world, even morally repugnant social arrangements (e.g. between masters and slaves) may be stable, at least for a time. But by understanding the principles underlying how social arrangements are sustained, we hope to identify points of psychological leverage that can help formalize strategies to bring a more just world into being.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
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