Author Reply: Emotion in Action – From Theories and Boxologies to Brain Circuits

Rebekah L. Blakemore
Department of Neuroscience, University of Geneva, Switzerland
Swiss Centre for Affective Sciences, University of Geneva, Switzerland

Patrik Vuilleumier
Swiss Center for Affective Sciences, University of Geneva, Switzerland
Department of Neuroscience, University of Geneva, Switzerland

Keywords
emotion–motor interactions, motivation, motor control, neural mechanisms

We are gratified to read that scholars commenting on our article accord with both the major need and potential great benefit to more systematically investigate functional links between emotion processes and action control. As emphasized in our review (Blakemore & Vuilleumier, 2017) and cogently discussed in the commentaries, a better understanding of intricate connections between emotion and action will illuminate the field of affective sciences to the extent that emotions constitute powerful signals that help guide behavior and ultimately shape actions. This endeavor will be greatly enriched by incorporating concepts and tools from the separate and mature field of motor control and by paying close attention to the neural circuits mediating these functional links.

A first challenge, clearly highlighted by the comments, will be to distinguish between different types and components of action, as this term incorporates a wide variety of phenomena—from the execution of voluntary movements, through to more reflexive motor behaviors, but also decision-making and goal-directed planning processes. These various aspects are subserved by different systems in the brain, and each may be influenced by or linked to affective processes through more than one mechanism. This is underscored by Hochstetter and Wong (2017) in their discussion of the article by Railton (2017). Furthermore, different emotions recruit at least partly different neural substrates, and may thus act at distinct processing sites, underpinned by different mechanisms, within the action control systems. It is therefore unlikely that emotion–action interactions can satisfactorily be described through a single conceptual framework, unless from a very broad and abstract perspective.

This is also why a simple "boxology" approach, as rightfully criticized by Eder (2017), will remain limited in scope and heuristic value if it does not incorporate precise mechanistic components referring to specific cognitive/affective processes and, whenever possible, their underlying neural implementation. If a complete theory must consider indeed that emotional foundations of actions concern not only overt bodily movements, but also more complex decision-making levels and various time scales (immediate reaction, long-term planning), then dissociable mechanisms will presumably have to be spelled out in order to account for different phenomena. More general perspectives, such as the statement put forward by Nanay (2017) that all actions are emotional in nature, bear the risk of remaining too vague, and eventually bring little progress in our mechanistic understanding of how and why emotions influence actions.

Likewise, while motivational processes provide a crucial functional link between emotion and action (Gendolla, 2017), it remains necessary to better dissect this link into components. Different motivational states may depend on different circuits, and some action may be triggered or modulated by emotion without the need of referring to motivational states in the sense usually implied by Gendolla and others. For example, some defensive motor behaviors during fear (amplified startle, freezing) can be elicited by direct projections from the amygdala to brainstem or premotor cortices (Davis & Whalen, 2001), presumably operating in a rather automatic manner but without the need to invoke the functional construct of motivational state as a distinct process mediating the elicitation of such motor phenomena. Thus, a motivational state of defense and avoidance is intrinsic to or coextensive with the motor responses characterizing the emotion of fear, but does not seem to necessarily precede these responses in a serially organized causal chain. On the other hand, some motivational states exist without being determined by emotions (such as thirst or hunger). Nevertheless, by highlighting several pathways from emotion to motivation, the

Author note: This work was funded by the Swiss National Center of Competence in Research for Affective Sciences (NCCR 51NF40-104897); and the Swiss National Science Foundation (SNF 320030-143764 to PV).
Corresponding author: Rebekah Blakemore, Department of Medicine, University of Otago, Christchurch, 66 Stewart Street, Christchurch 8011, New Zealand.
Email: rebekah.blakemore@otago.ac.nz

framework proposed by Gendolla (2017) provides an initial and useful distinction between different mechanisms through which emotion processes may interact with motivational systems in order to influence action.

Moreover, motivational states can have different sources, connected to current goals, memory, mood, and/or other physiological parameters, which are implemented in partly different brain circuits and thus likely to guide actions in different ways. These effects might be fruitfully explored though neuroscience approaches that characterize brain states in relation to emotion in terms of variations in the functional connectivity or functional interactions within and between brain networks (Kragel & LaBar, 2016). Accordingly, emotions can induce selective and time-dependent (sometimes long-lasting) changes in the functional coupling between different brain areas (Eryilmaz, van De Ville, Schwartz, & Vuilleumier, 2014). These connectivity changes could subsequently bias perception or memory (Qiao-Tasserit et al., 2017), and similarly bias action by modulating particular brain network connections. Future research could investigate how action and decision-making are modulated by changes in brain network connectivity patterns that follow transient emotional events, and which connectivity changes predict action changes. Such modulation of connectivity patterns would not only constitute a plausible mechanism through which motivational states emerge from emotions, outlast their transient triggers, and then guide behaviors, but also accord with the view expressed by Nanay (2017) that emotion can influence thresholds for action execution, beyond the spinal cord. Synaptic modulations across neuronal circuits could account for emotional and motivational effects on action control operating at different time scales. Characterizing these effects in the temporal domain also requires a better mechanistic understanding of their underlying neural substrates.

In sum, as illustrated by the various perspectives highlighted in this issue of *Emotion Review*, time seems ripe to expand emotion and motivation theories by connecting these fields to well-established frameworks of action control, and to build on mechanistic accounts that link motor function and decision-making to precise cognitive and/or neural processes. As proposed in our review, the richness and complexity of emotion–action interactions will require distinguishing different components and steps in action control (e.g., intention, execution, inhibition, or monitoring), and relating them to specific brain circuits beyond general boxology models. Current motor control theories that have generated sophisticated computational and neuroanatomical models can yield important new insights into the functional relationships of emotions with action and motivation, and in turn they will be greatly enriched by incorporating emotion and motivation signaling in motor control processes.

References

Blakemore, R. L., & Vuilleumier, P. (2017). An emotional call to action: Integrating affective neuroscience in models of motor control. *Emotion Review*, *9*(4), 299–309.

Davis, M., & Whalen, P. J. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry*, *6*, 13–34.

Eder, A. B. (2017). Comment: From boxology to scientific theories: On the emerging field of emotional action sciences. *Emotion Review*, *9*(4), 343–345.

Eryilmaz, H., van De Ville, D., Schwartz, S., & Vuilleumier, P. (2014). Lasting impact of regret and gratification on resting brain activity and its relation to depressive traits. *Journal of Neuroscience*, *34*, 7825–7835.

Gendolla, G. H. E. (2017). Comment: Do emotions influence action? Of course, they are hypo-phenomena of motivation. *Emotion Review*, *9*(4), 348–350.

Hochstetter, G., & Wong, H. Y. (2017). Comment: Affective control of action. *Emotion Review*, *9*(4), 345–348.

Kragel, P. A., & LaBar, K. S. (2016). Decoding the nature of emotion in the brain. *Trends in Cognitive Sciences*, *20*, 444–455.

Nanay, B. (2017). Comment: Every action is an emotional action. *Emotion Review*, *9*(4), 350–352.

Qiao-Tasserit, E., Garcia Quesada, M., Antico, L., Bavelier, D., Vuilleumier, P., & Pichon, S. (2017). Transient emotional events and individual affective traits affect emotion recognition in a perceptual decision-making task. *PLoS ONE*, *12*(2), e0171375. doi:10.1371/journal.pone.0171375

Railton, P. (2017). At the core of our capacity to act for a reason: The affective system and dynamic model-based learning and control. *Emotion Review*, *9*(4), 354–355.