notion of content. This is ironic, since if Hutto and Myin are right, a properly con-
strued enactivist has precisely the right
shape to deal with representational content,
namely by showing how to account for it
where it is genuinely present. Besides, as
“radical” as such enactivism might look, it
should not be discredited by the fact that it
breaks with prominent strands of research,
or ways of talking in the sciences of cogni-
tion, including artificial intelligence, or if it
runs counter to cherished intuitions. In fact,
leaves should be taken out of The Embodied
Mind, where Varela, Thompson and Rosch
(1991: 133) stated: “why do we assume that
cognitive science cannot call into question
these notions of representation and infor-
mation not just philosophically but in its
day-to-day research?”

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Active Vision: A Broader Comparative Perspective
Is Needed

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> Upshot • We sympathize with the view
that visual information is often acquired
by active sampling of the environment,
for example, through scanning move-
ments. Not all vision is (en-)active, how-
ever – humans can capture important
details of a visual scene at a glance, for
example. The strategies of active sam-
pling in various animals depend substan-
tially on the structure of their visual sys-
tems and the representational capacities
of their brains.

Humans are capable of identifying
certain elements of visual scenes at a glance
(Thorpe, Fize & Marlot 1996; Kirchner &
Thorpe 2006), using parallel search (Wolfe
2000). The rapid categorization of the kind
seen in humans and monkeys might rely
on pre-attentive feed-forward processing
of low-level features (Joubert et al. 2009;
Walker, Stafford & Davis 2008). Extraction
of image components at a glance in primates
implies a time course that seems compatible
with only a single sweep of sensory informa-
tion along the known delays of the visual
system (VanRullen & Thorpe 2002). This
indicates that an active exploration of the
visual environment (e.g., by saccades or ac-
tive head or eye movements) is at least not
necessary for all visual processing.

This fundamentally anticipates the idea that
animals use spectral information in differ-
ent ways, depending on ecology and sensory
apparatus, as experimentally confirmed
first by John Lubbock’s (1882) discovery
of UV sensitivity in insects. There is much
more variety of color vision systems across
animals than Palacios, Escobar & Céspedes
acknowledge: even within the vertebrates,
numbers of spectral receptor types range
from one to five, with some species of inver-
tebrates having substantially greater diver-
sity still (Skorupski & Chittka 2011; Thoen
et al. 2014). There are at least as many “col-
ored worlds” as there are spectral receptor
systems across animals.

> 2 > Notions of links between action and
perception likewise date back to the
19th century; see, e.g., the explorations by
Johannes Purkinje (1825) to explain why
active, voluntary movement of the eye does
not cause a perception of movement of the
visual scene, while pressing the eye with a
finger does induce perceived motion. This
phenomenon of the “efference copy” (von
Holst & Mittelstaedt 1950) has been stud-
ied neurophysiologically in crustaceans
(Skorupski & Sillar 1986) and insects, where
its neural underpinnings are now under-
stood in unparalleled detail (Kim, Fitzger-
ald & Maimon 2015). Spontaneous turn-
ing movements in tethered flies could be
conceived of as active visual probing of the
environment, and the perception-as-action
perspective fits comfortably with studies on
spontaneous actions and decision-making
with small brains (Brembs 2011). Whether
this sweeps away the theoretical need for
representations in understanding cognition
remains perhaps questionable; the context-
ual notion of representation in a weak
sense, put forward by the authors of the tar-
get article, strikes us as useful.

> 3 > We agree with Adrián Palacios,
María-José Escobar and Esteban Céspedes
that “the question about whether color is
an objective feature of the world has lost
relevance” (§35). However, we respect-
fully disagree that the enactivist perspective
(Tompson, Palacios & Varela 1992) gave
birth to this notion. As early as Hermann
Grassmann’s (1853) mixture laws, it was
clear that fundamentally different physical
stimuli could generate the same perceptual
states. Turning to comparisons with other
animals, almost 150 years ago, John Strutt
suggested:

** “The assumed attractiveness of bright colors to
insects would appear to involve the supposition
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the same as our own. Surely this is a good deal to
take for granted.” ** (Strutt 1874: 6)

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In some animals a link between action and perception has been demonstrated empirically. For example, pigeons acquire stereotyped approach routes when learning visual pattern discrimination tasks, and fail at these tasks when they are prevented from using their accustomed route (Dawkins & Woodington 2000). In other behavioral contexts, pigeons actually move their heads in characteristic ways ("head-bobbing") to stabilize their image during forward locomotion (Theunissen & Troje 2017). Stomatopod crustaceans are an extreme case since their many types of spectral photoreceptors are arranged in tiers across their eyes – hence their only possibility to obtain color information is by making scanning movements, pointing the different spectral receptor types at the target sequentially (spectral scanning; Tohen et al. 2014).

Active vision has also been suggested to play a role in color perception of bees (Skorupski & Chittka 2011). As ommatidia contain a variety of different sets of color receptor types (Spathe & Briscoe 2005; Wakakuwa et al. 2005), a single-colored object might be perceived as consisting of multiple pixels each with different colors – unless insects move their eyes over the object to generate a temporal integration (Skorupski & Chittka 2011). This could explain why bees, while they can discriminate distinct colors that are only briefly flashed (25mm), need longer integration times (50ms) for reliable discrimination when colors are similar (Nityananda, Skorupski & Chittka 2014).

It could be that a single "sensory snapshot" is less useful for a miniature brain simply because there is less capacity for off-line processing (processing involving significant neural delays). In active perception, the time taken to build up a picture of the environment will depend on how much can be sampled at once, and in a miniature brain there may be less capacity to process a single sensory snapshot, and consequently a greater dependence on continuous online sampling of the scene. It is possible that reduced representational capacity (in the weak sense of representation intended by Palacios, Escobar & Céspedes) may lead to fundamentally different perceptual sampling strategies in large and small brains. However, in certain highly active miniature-brained animals, such as flies and bees, reduced representational capacity may be compensated for by higher real-time sampling of their environment (Chittka & Skorupski 2011).

In small nervous systems, active vision could compensate for limitations imposed by limited detail provided by reduced receptor arrays. With a dynamical-systems approach it is possible to show that an array of only seven photoreceptors can classify circles vs squares, given self-generated movements (Beer 2003). In the biological realm, Drosoptilidae larvae, with only 12 photoreceptors, can distinguish movement of conspecifics from other visual signals (Justice et al. 2012). Moving to bees, we find eyes with image-forming optics, but the 8,000 ommatidia of a bee's eye would seem to provide rather a poor image (compared to that generated by millions of rods and cones in the human eye). On the other hand, the visual learning abilities discovered in bees seem rather remarkable. Could it be that active vision strategies enable bees to overcome the poor spatial resolution implied by the optics of the compound eye? Indeed, there is now evidence that bees require active scanning movements for all but the most basic visual discriminations (Nityananda, Skorupski & Chittka 2014).

In an animal with limited storage or representational capacity, part of image representation could be moved to its environment, using active vision. For example, a discrimination task of square versus circle could be conventionally solved by storing images of the two shapes (either a pixel-by-pixel image or some compressed representation that highlights key features) and comparing them. Alternatively, to ease demands in representational capacity, the task could be solved by comparing what the shapes induce you to do. For example, if you have a habit of scanning contrasting boundaries during approach flight (which bees do), then it would suffice to scan only a tiny section of the shape to make the discrimination. The circle then becomes "that which makes me move in an arc" and the square "that which makes me move in a straight line."

In conclusion, we agree that in many animals and many scenarios, to perceive something is to actively sample it, and that perception is constituted in implicit knowledge (accumulated both phylogenetically and ontogenetically) of how the properties of the sensory motor apparatus result in changes in the sensory input during perceptual sampling (for example, eye movements in humans). This account places more of the burden of perception in the world itself, rather than in putative mental representations. However, the extent to which this applies depends on the task, as well as the particular visual system and the representational capacity of the animal; large-brained animals such as humans might in some cases bypass the need for active sampling, whereas small-brained animals such as bees are strictly dependent on it.

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