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Neural Representations Observed

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Abstract The historical debate on representation in cognitive science and neuroscience construes representations as theoretical posits and discusses the degree to which we have reason to posit them. We reject the premise of that debate. We argue that experimental neuroscientists routinely observe and manipulate neural representations in their laboratory. Therefore, neural representations are as real as neurons, action potentials, or any other well-established entities in our ontology.

Keywords Representation · Neural representation · Neuroscience · Experiment · Teleosemantics

1 From Theoretical Posits to Observables

Representations are internal states that "stand in" for X so as to guide behavior with respect to X. For example, a representation of yogurt in your refrigerator "stands in" for the yogurt and guides your behavior with respect to the yogurt. In other words, representations are entities that have both a semantic content—e.g., "there is yogurt in the refrigerator"—and an appropriate functional role (Ramsey 2016), and the specific functional role they play depends on their semantic content.

Representations are traditionally construed as unobservable entities posited by a theory or model to explain and predict behavior. The theory may be either folk psychology (e.g., Sellars 1956) or scientific psychology (e.g., Fodor 1975, 1981). The debate centers on whether the representations posited by some theory or model

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are real, whether they have semantic content, and whether their semantic content plays a functional role.

Several grades of antirealism about representation have been proposed. Some argue that representations are real entities that play a functional role but their semantic content is merely a matter of interpretation—it is not a real property and plays no functional role (e.g., Dennett 1987; Cummins 1983, 1989). A closely related view is that representations are real in the sense that there are internal states individuated by what *we* take them to represent, but the internal states themselves have no semantic content (Chomsky 1995). Finally, there is full-blown representational eliminativism: representations have no place in a mature science of cognition, which will explain and predict behavior without appealing to representations (Stich 1983; Brooks 1991; van Gelder 1995; Keijzer 1998; Garzon 2008; Chemero 2009; Hutto and Myin 2013; Downey 2017; Varela et al. 2017).

More recently, the debate about representation has come to include cognitive and computational *neuro*science (Churchland 1986; Churchland 1989, 2012; Churchland and Sejnowski 1992; Bechtel 2008; Milkowski 2013; Boone and Piccinini 2016). In spite of this shift, the debate continues to center on representations qua theoretical posits. Skeptics argue that neuroscientific models dispense with representations, or at least with representations properly so called (Ramsey 2007; Burge 2010; Hutto and Myin 2014; Raja 2017). Other skeptics argue that, even if neuroscientific models do not dispense with representations, semantic content is dispensable in the sense that it plays no causal or explanatory role (Egan 2014). Supporters reply that representations, complete with semantic content, do play an explanatory role within some neuroscientific models (Shagrir 2012, 2017; Sprevak 2013; Colombo 2014; Clark 2016; Gładziejewski 2016; Kiefer and Hohwy 2017; Williams 2017; Maley 2017).

Participants in this debate have mostly neglected the role of representations in experimental neuroscience. Some philosophers of neuroscience discuss experimental practices (Bickle 2003; Craver 2007; Sullivan 2009) but they do not focus on neural representations. When philosophers discuss neural representations within experimental neuroscience, typically they mention experimental neuroscience either as inspiring information-based theories of content (e.g., Ramsey 2016, 7) or as supporting some particular theory, model, or explanation (e.g., Grush 2004; Sullivan 2010). Two exceptions are Churchland and Sejnowski (1992, Chap. 4) and Bechtel (2008, Chap. 5; 2016), who suggest that experimental evidence supports the existence of neural representations. We will build on this insight.

Since Ian Hacking's (1983) groundbreaking work, philosophers of science have pointed out that experimental science often has a life of its own: through observation and manipulation, experimentalists can establish that an entity exists (Galison 1987, 1997; Staley 1999; Franklin 2002, 2013; Chang 2004; Weber 2005, 2014; Franklin and Perovic 2016). To be sure, theories and experiments coevolve, and theories are often used in designing experimental procedures, calibrating instruments, and processing and interpreting data. Nevertheless, experimentalists use theories and methods that are often established independently of current points of dispute.

For example, in the nineteenth and early twentieth Century there was a dispute about whether nerve fibers form a continuous network or are made of distinct yet interconnected cells. Resolving it in favor of the neuron doctrine required the development of reliable staining techniques, electron microscopy, and other experimental techniques. Later on, recording the precise shape of action potentials required the development, with the help of Ohm's law, of sensitive means of measuring millivolt deflections across individual nerve fibers (Hodgkin and Huxley 1939). Yet Ohm's law, the reliability of staining techniques and microscopes, and other background conditions were established independently of debates about neuronal connectivity and action potential generation. In addition, neurons and their action potentials can be recorded and manipulated in a variety of ways using a variety of techniques. By now, it is a well-established experimental observation both that neurons are distinct cells and that they fire action potentials.

In this paper, we reframe the debate on representation by focusing on standard results from experimental neuroscience. Experimental neuroscientists began talking about representations in the nervous system almost a century before the beginning of the cognitive revolution, which is so often associated with the contemporary dispute. At first neuroscientists posited what are now called motor representations (Hughlings Jackson 1867, 1868); later they added what are now called sensory representations (Horsley 1907, 1909). While neural representations began as theoretical posits, neuroscientists have long reached the point where they routinely observe and manipulate representations using multiple methods and techniques in multiple model systems, just as they observe and manipulate neurons and action potentials. The techniques and procedures they use are validated independently of any debates about neuronal representation. As a result, there are at least three kinds of empirically well-established neural representations: sensory representations, representations uncoupled from current sensory stimulation, and motor representations.[1]

In the next section, we will articulate the notion of representation at play, allaying concerns that neuroscientists use an overly permissive notion of representation (Ramsey 2007). In the following three sections, we will review some of the many experimental observations on sensory, uncoupled, and motor representations. With that, we rest our case.

2 Representation

For something to count as a representation, it must have a semantic content (e.g., "there is yogurt in the fridge") and an appropriate functional role (e.g., to guide behavior with respect to the yogurt in the fridge). Let's look more closely at these two features of representation.

Let's begin with functional role. A representation's role is to serve as a "stand in" for X so as to guide behavior with respect to X. Following Ramsey (1931),

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[1] This is not an exhaustive list. For instance, we won't discuss neural representation of space (Andersen et al. 1997; Moser et al. 2008).

Dretske (1981, 197) describes beliefs as internal maps by which we steer (cf. Armstrong 1973; Dretske 1988, 78). Craik (1943) describes representations as mental models that we use to plan and guide our behavior. This perspective is sometimes cashed out more formally in terms of a functioning homomorphism (Gallistel 1990, 2008; Gallistel and King 2009) or, equivalently, exploitable similarity (Godfrey-Smith 1996; Shea 2007, 2014; Gładziejewski and Miłkowski 2017).[2]

Along with a fitting functional role, a representation has semantic *content* (Anscombe 1957; Searle 1983), which is either indicative or imperative (Millikan 1984). Representations with *indicative* content represent how the world *is*; they are satisfied to the degree that they track the actual state of the world. By contrast, representations with *imperative* content represent how the world *will be*; they are satisfied to the degree that the world comes to track them (cf. Mandik 2003).

Indicative representations include *sensory* representations. For example, a sensory representation of a small dark spot moving to the left is satisfied to the degree that there is indeed a small dark spot moving to the left. If there is no such object, or if it's moving upward, the system has *misrepresented* the environment.

Imperative representations include *motor* representations, whose function is to *bring about a new state of affairs* by generating behaviors. They are satisfied to the degree that the body appropriately carries out the commands. For example, the command to pick up an orange is satisfied just in case the agent picks up the orange. Since we are focusing on neural representations, from now on we will restrict ourselves to sensory and motor representations, leaving other kinds of indicative and imperative representations aside.

To specify the content of representations more precisely, we will draw from previous theories of representational content. The best-developed and most plausible theory of representational content in biological systems is called teleosemantics (Stampe 1977; Dretske 1988; Fodor 1987, 1990, 2008; Millikan 1984, 1993; Ryder 2004a, forthcoming; Neander 2017; this literature is surveyed in Adams and Aizawa 2010; Neander 2012; Neander 2017). Different versions of teleosemantics differ in their details; this is not the place to discuss their differences (cf. Neander 2017). Here we adopt a specific version of the theory that incorporates both functional role and semantic content.

In the philosophical literature, most of the attention has gone to sensory representations (exceptions include Millikan 1984, 1993; Papineau 1984, 1993; Mandik 2003; Butterfill and Sinigaglia 2014; Ferretti 2016; Mylopoulos and Pacherie 2017). In experimental neuroscience, motor and sensory representations are both extremely important, so we discuss both. We also will discuss indicative representations that are not directly coupled to current sensory stimulation.

When it comes to sensory representation, teleosemantics takes an *informational* form (Neander 2017). That is, teleosemantics assigns semantic content to sensory representations based on the natural semantic information they carry. A state (or

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[2] Similar notions of representation are defended by Shepard and Chipman (1970), Swoyer (1991), Cummins (1996), Grush (2004), O'Brien and Opie (2004), Ryder (2004, forthcoming), Bartels (2006), Waskan (2006), Ramsey (2007), Bechtel (2008), Churchland (2012), Shagrir (2012), Isaac (2013), Hohwy (2013), Clark (2016), Morgan (2014) and Neander (2017, Chap. 8).

signal) S carries natural semantic information that P just in case it raises the probability that P (Scarantino and Piccinini 2010; Piccinini and Scarantino 2011; Scarantino 2015). This can be quantified in different ways, for instance using mutual information (Thomson and Kristan 2005). The function of a sensory system is to carry natural semantic information about events in the local environment, and the neuronal signals that transmit this information can subsequently guide how the agent responds to such events.

Thus, our version of informational teleosemantics for sensory representations is this:

> (SR) A state (or signal) S within an agent's representational system R *indicatively represents* that P $=_{\text{def}}$ A function of R is to produce S, such that S carries natural semantic information that P and S can guide the agent's behavior with respect to the fact that P.

In other words, a state S indicatively represents that P just in case S tracks that P, where tracking that P consists in carrying the natural information that P, and the system R that produces S does so in order to guide the organism's behavior with respect to P. That is the system's *indicative function*. The content of sensory representations will track the state of the world to the degree that the system fulfills its indicative function. If S represents that P but it is not the case that P, then S misrepresents the state of the world.

Motor representations have a different function, and hence a different type of semantic content, than sensory representations. They do not serve to carry information about the world into the system, but to *generate new states of the world*. That is, they carry imperative, not indicative content.

A motor representation is satisfied if the world *becomes* the way it is represented to be. Here is our version of teleosemantics for motor representations:

> (MR) A state (or signal) S within an agent's representational system R *imperatively represents* that P $=_{\text{def}}$ A function of R is to produce S, such that S causes that P.

In other words, a state S imperatively represents that P just in case the system that produces S has the function of producing S in order to bring it about that P. That is the system's *imperative representational function*. The world will track the content of motor representations to the degree that the system fulfills its imperative representational function. The environmental state that P is the *goal* of the internal state, which can be used to assign an error measure to the behavior. If S represents that P but P doesn't come about, then there was a mistake in execution.

In the rest of the paper, we will provide evidence that sensory and motor representations are no longer mere theoretical posits: they are routinely observed and manipulated by experimental neuroscientists. Observing and manipulating neural representations means establishing, via experimental observations and interventions, that a neural signal fits the criteria for representation. For sensory representations, the criteria are that (1) the signal carries information about some state external to the system, (2) there is a systematic mapping between a range of similar signals and a range of similar external states, and (3) the system uses these internal states to guide behavior. For motor representations, the criteria are that (4) the signal correlates with a future state of the environment (where the environment includes the body), (5) there is a systematic mapping between a range of similar signals and a range of similar future states of the environment, and (6) such signals actually *cause* movements that bring about the future states of the environment.

As we shall point out, (1)–(6) have been established again and again, beyond reasonable doubt, in many different neural systems using many independent techniques. Therefore, even if experimental neuroscientists had *not* already reached consensus that neural signals that satisfy the above accounts are representations—*which they have*—that's what they *should* conclude. Experimental neuroscientists are *in fact* discovering, observing, and manipulating neuronal representations in the sense discussed above.

Before getting into the details, let's briefly consider some of the methods used in physiology and anatomy, though obviously we cannot be exhaustive. Physiologists *measure* neuronal activity at scales from the very small (patch clamp to record currents and voltages generated in single neurons or even patches of neuronal membrane, extracellular recordings, calcium- and voltage-sensitive dye imaging), up to very large (EEG or fMRI) (Churchland and Sejnowski 1992; Kandel 2013). In sensory systems, such neural activity is observed to correlate with some specific features of an external stimulus; this establishes what the activity carries semantic information about and that there is a broader mapping between similar neural signals and similar external states. To examine the causal role of individual neurons or neuronal areas and show that it affects downstream processing and ultimately behavior is more complicated: it typically involves ablation studies, or manipulating currents and voltages in individual neurons (current and voltage clamp) or clusters of cells via extracellular microstimulation (Kandel 2013). Recent years have also seen the explosion of the extremely powerful technique of optogenetics, in which genetically targeted classes of neurons are excited or inhibited via light, in real-time, using light-activated ion channels (Yizhar et al. 2011). Transcranial magnetic stimulation is sometimes used to noninvasively perturb circuits on much larger spatial scales (Hallett 2000).

Neuroanatomy lets us probe the closely related *structural* features of neurons and circuits at multiple scales, which can be useful for determining the trajectory of information flow and causal relationships in a system, including its connections within the brain and to states of the external environment. At the lowest scale is scanning electron microscopy (EM), the gold standard. Not only does it reveal the fine-grained structural features of individual neurons (such as dendritic tree organization), but it has recently given birth to *connectomics* (the large-scale study of connections among all neurons in a system, or part of a system such as a piece of the retina). Connectomics was inaugurated by the recent development of serial block-face scanning EM (Denk and Horstmann 2004), but is also being pursued with the help of diffusion-tensor imaging in MRI (Mori and Zhang 2006). Tract tracing is also pursued with more traditional methods such as anterograde and retrograde tracing that allows you to find the neurons presynaptic to, or postsynaptic to, a given neuron, respectively (Purves 2018; Wickersham et al. 2007). There are also traditional histological techniques such as filling individual neurons with dye to reveal their morphology, and staining of sliced sections of the brain, which helps reveal the brain's gross cytoarchitectural features. Obviously, anatomy and physiology are closely related: if two areas are revealed, via anterograde tracing techniques, to be tightly connected, then they will be a good candidate for dual intracellular recordings to find functional chemical or electrical synapses.

Before getting to the empirical evidence, a few caveats are in order. First, note that we will be discussing research at two levels of resolution. On one hand, we will sometimes give a panoramic, high-level overview of the neurobiology of representational systems, without going into much detail about the evidence that supports (1)–(6) above. This is meant to give a sense of the ubiquity of neural representational systems, including some that have not received much attention from philosophers (e.g., the birdsong system). On the other hand, in each section we will also zoom in on one example to give a more detailed sense of the types of experiments and reasoning that are involved in discovering and manipulating neural representations (for a couple of more detailed case studies, see also Bechtel 2016; Burnston 2016a, b).

Second, our account is limited to sensory, uncoupled, and motor neural representations. We are not giving an account of what is distinctive about *mental* representations. We are not attempting to explain full-blown mental or linguistic intentionality, including the ability to represent nonexistent objects like unicorns or abstractions like numbers, the possession of non-natural meaning in Grice's (1957) sense, or the ability to attach different senses to the same referent (Frege 1892). However, our framework does provide building blocks that will likely be part of a complete theory of mental representation and intentionality, given suitable extensions (Neander 2017; Morgan and Piccinini 2017; Piccinini forthcoming).

Third, we are not endorsing the language of thought (Fodor 2008; Schneider 2011), connectionism (Churchland 1989; Churchland and Sejnowski 1992; Clark 1993; Horgan and Tienson 1996), or any other framework from theoretical psychology. Our argument is focused on the best available evidence from experimental neuroscience. The theory we employ is largely limited to the basic notion of representation articulated above in combination with some basic ideas from information theory (Cover and Thomas 2006) and control theory (Wolpert and Miall 1996).

Fourth, accepting neural representations does not negate that cognition is dynamical, embodied, and embedded (Beer and Williams 2014; Clark 1997; Clark and Toribio 1994; Eliasmith 2001; Horgan and Tienson 1992; Hotton and Yoshimi 2010). Neural representations are states of dynamical systems, which are typically tightly coupled to the organism's body and environment. As we shall see, representations acquire semantic content thanks to the coupling between nervous systems, bodies, and their environment. Perhaps biological minds also include aspects of the body and environment beyond the neurocognitive system, but this will not influence the points herein.

Fifth, we will largely sidestep questions about phenomenal consciousness. Perhaps a complete theory of intentionality requires taking consciousness into account (Horgan and Tienson 2002; Loar 2003; Kriegel 2013; Bourget and Mendelovici 2017). Either way, neural representations are not sufficient to generate phenomenal consciousness. One, in the neuropsychological condition known as *blindsight*, people lacking visual consciousness due to V1 damage can still successfully perform simple visual discrimination tasks, because visual information reaches the brain via subcortical processing streams that never reach consciousness (Leopold 2012). Two, as we will see, in binocular rivalry, one of the retinal representations of the stimulus is not perceived; even in V1 the bistable representational dynamics continue to occur under anesthesia, when subjects are unconscious (Xu et al. 2016). Three, consider the old chestnut of whether you were aware of the tactile information coming in from the bottom of your feet just before reading this sentence. The information was there, making its way into your nervous system. What ingredients, beyond such low-level sensory representations, are needed to bring such information into conscious awareness? There has been a lot of research on this topic, but it is clear that neural representations are not sufficient for conscious awareness. Hence, we will not be entering debates about consciousness, and reject any view in which consciousness is necessary for the existence of representational content.

3 Sensory Representations

When neuroscientists discuss sensory representations, they mean activation patterns in the nervous system that carry information about the current environment, are part of a broader mapping between neural states and states of the world, and help guide behavior. For instance, activity in the topographic map of the visual environment contained in primary visual cortex may carry the information that the traffic light has just turned green, and this activity is used by the brain to decide to do things like pull the foot off the brake pedal. This conforms with (SR), our teleosemantic account of indicative content.

Experimental neuroscientists have discovered sensory representations at multiple levels of organization in the nervous system, from low-level sensory representations in the retina to higher-level representations many steps removed from the periphery. Even the leech has tactile representations that guide behavior with respect to touch (Lewis and Kristan 1998b). Sensory representations provide the basic informational intersection between the local environment and the brain, giving the brain indirect access to the environment and providing organisms fallible but reliable information channels upon which to base decisions. In the next few subsections, let's examine sensory representations using examples from the visual system.[3]

3.1 Image Compression in the Retina

The eye projects the visual scene onto the photoreceptor mosaic. The photoreceptors in the retina convert a specific type of physical stimulus—light—into signals that can be used by the rest of the nervous system to guide behavior.

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[3] For a fuller treatment, see Hubel and Wiesel (2005), Rodieck (1998) and Wandell (1995).

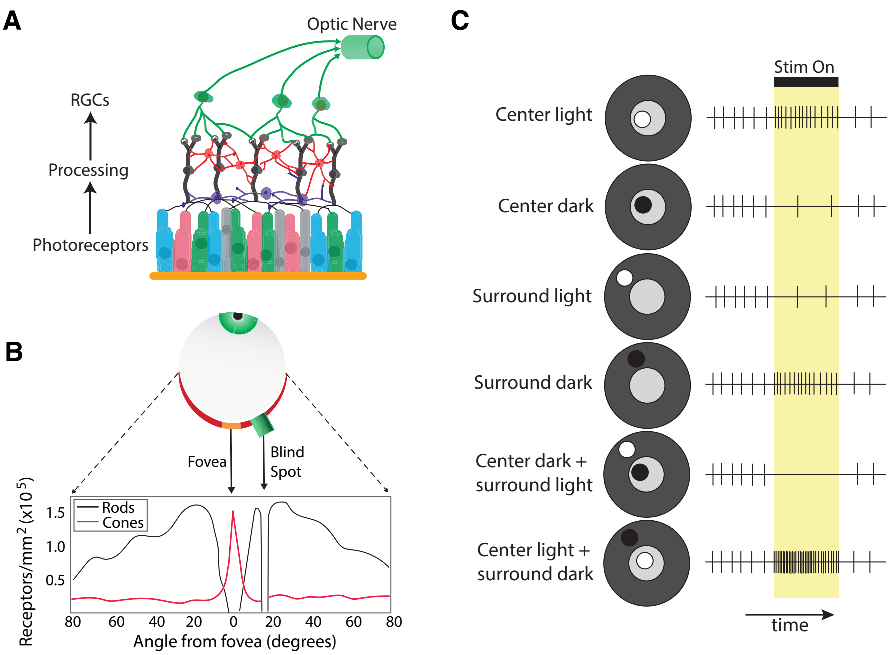

Fig. 1 Retinal representation of the visual world. **a** Retinal wiring diagram. Light activates photoreceptors, and information flows through multiple neuronal processing stages before reaching the retinal ganglion cells (RGCs), whose axons leave the eye via the optic nerve. **b** Rod and cone density as a function of distance from the fovea. The blind spot is where photoreceptor density is zero, as that is where the optic nerve exits the eye. Figure based on Wandell (1995), Fig. 3.1. **c** Cartoon showing response properties of an on-center, off-surround RGC. The entire receptive field is about the size of a dime held at arm's length from the eye. Each neuron has some background firing rate before a stimulus is presented. When light levels are incremented in the receptive field center, or light is dimmed in the surround, the firing rate increases. Conversely, when brightness is incremented in the surround, or dimmed in its center, the firing rate *decreases*: Center and surround responses combine, as shown in the bottom rows. For instance the cell responds maximally when light is incremented in the center, and dimmed in the surround (bottom row)

Photoreceptors are not evenly distributed across the retinas as depicted in Fig. 1a, but highly concentrated in one region, the *fovea*, as shown in Fig. 1b. Photoreceptor density drops off precipitously as you move away from the fovea into the periphery of the visual field. The optic nerve exits the eye from the back the retina. In that region of the retina, there are *no* photoreceptors, so an object projected to this region of the retina will disappear from view. This region is called the *blind spot*.

But the retina is much more than a sheet of photoreceptors. It is a complex information processing system in its own right, where a good deal of convergence and integration of information occurs (Fig. 1a; for a review see Dowling 2012). While each human eye contains about 100 million photoreceptors, only one million axons make their way through the optic nerve. Hence, information from multiple photoreceptors is pooled and transformed, in complex ways across multiple processing stages, until the signals reach the retinal ganglion cells (RGCs) (Masland 2012). The RGCs are the output neurons of the retina—their axons snake their way to the brain via the optic nerve (Fig. 1a). Thus, the brain receives a kind of compact summary of the original information stream transduced by the photoreceptor mosaic.

Recording from RGCs shows that they are not merely light detectors but *feature detectors* (Sanes and Masland 2015) that respond to specific features present in the visual field in a circumscribed region of space, a region of space known as that neuron's *receptive field* (*Spillmann* 2014). RGCs tend to respond to *spatial contrast* in light intensity, or *differences* in light levels. One classical type of RGC has what is known as an 'on-center/off-surround' receptive field, and responds with a brisk burst of activity if you present a bright spot of light surrounded by a dark annulus (Fig. 1c) (Dowling 2012). There is an entire subfield in visual neuroscience devoted to the study of how such receptive fields are assembled in retinal circuits (Briggman et al. 2011; Ding et al. 2016; Mangel 1991).

While neuroscientists rarely say that individual photoreceptors *represent* the visual world in primary research publications (Baylor 1987; Korenbrot 2012), once we reach the RGCs, such attributions are pervasive (Li et al. 2014; Roska and Werblin 2001; Soo et al. 2011; Wandell 1995). That is, once we reach neurons with receptive fields that compactly encode information about a relatively high-capacity stimulus space, the language of representation is used frequently. This conforms to the notion of indicative representation (SR) discussed above in Sect. 2, in which neuronal processes carry information into the brain, forming an internal map of an aspect of the environment, and this map is used to control behavior.

3.2 Visual Maps in V1 and the Representation of the Blind Spot

Once leaving the eye, visual information flows through the optic nerve into the CNS, where it makes its way to the primary visual cortex (V1) (Fig. 2a). The map of the visual world in V1 is retinotopically organized, such that two points close to one another on the retina are also represented by nearby positions in V1 (Fig. 2b).

The representation of visual space in V1 is not an exact mirror of the visual world, but highly biased. For instance, there is much more cortical real estate devoted to the foveal region compared to the periphery. Further, the neurons representing the fovea also have smaller receptive fields (Daniel and Whitteridge 1961; Dow et al. 1981; Tootell et al. 1988). That is, V1 yields a distorted picture of visual space, with the fovea receiving disproportionately large amount of cortical territory, with more spatial acuity, compared to the periphery (Tootell et al. 1988).

In general, V1 receptive fields are more complex than those found in RGCs, with neurons tuned to more complex properties such as movement, oriented bars, and depth (Hubel and Wiesel 1968). V1 contains multiple fine-grained topographically organized *feature maps* of such properties embedded in the larger-scale retinotopic representation of space. For instance, those neurons selective for horizontally oriented bars tend to cluster together in *cortical columns* in V1, and nearby columns contain neurons that are tuned to similar orientations (Fig. 2c).

What is the fate of the blind spot within V1? Dennett argued that the blind spot is not explicitly represented in the brain, as much as *ignored* (Dennett 1991). In fact, experiments using electrophysiology and fMRI have shown that the blind spot is

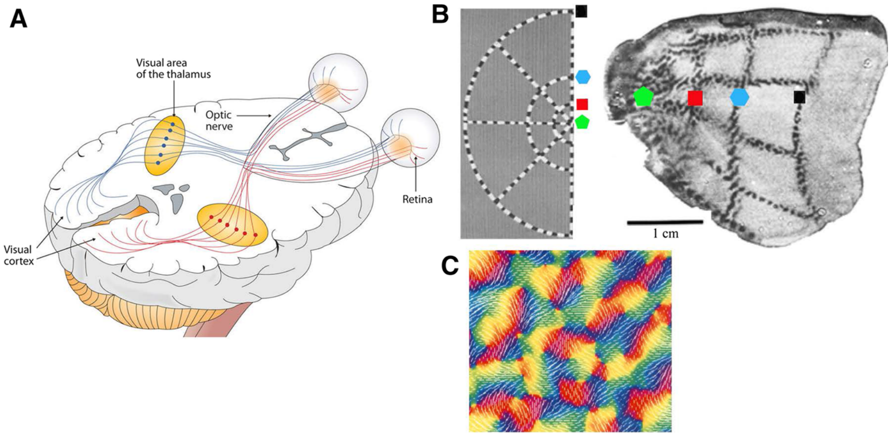

Fig. 2 Main visual pathway. **a** The visual pathway carries information from the retina to the thalamus via the optic nerve. From the thalamus, visual information makes its way to primary visual cortex (V1). (Reproduced with permission from Stangor 2011). **b** Topographic organization of V1. On the left is the visual stimulus that was presented on the left half of a video screen. On the right is the corresponding metabolic activity profile in the right-hand side of V1. The colored polygons on the left are shown for reference: for instance, the green pentagon is next to the foveal region of the visual field, and is also shown in the foveal region of V1 on the right. The topographic organization is maintained, but with more territory devoted to regions closer to the fovea. Even though the pentagon and square are very close together in visual space, they are relatively far from one another on the surface of the cortex. (Reproduced with permission from Tootell et al. 1988). **c** Orientation map in V1. A flattened view of V1, as in 2B, but here each color corresponds to a region of V1 with neurons tuned to bars of a particular orientation. For instance, the red areas tend to prefer vertical edges, while the green regions contain neurons that prefer horizontally oriented bars. (Reproduced with permission from Blasdel 1992)

actively represented in V1 (Awater et al. 2005; Azzi et al. 2015; Komatsu et al. 2000; Matsumoto and Komatsu 2005). For instance, one study performed single-unit recordings in the region of V1 corresponding to the blind spot in capuchin monkeys (Matsumoto and Komatsu 2005). After finding the ‘hole’ that corresponds to the blind spot in the V1 topographic map—namely, neurons that do not respond to stimuli that fall completely within the blind spot—they meticulously mapped these neurons’ receptive fields using standard techniques: they presented a range of stimuli (e.g., randomly flickering lights, or oriented moving bars) to the monkey. Interestingly, they found a *topographic map* of visual space *within* the blind spot that serves to preserve the general topography found in the rest of V1 (Matsumoto and Komatsu 2005).

This representation is, by definition, not a direct response to retinal activation in the relevant region of visual space. It seems to be due to completion mechanisms that “fill in” the blind spot, interpolating based on the cues at its edges. This amounts to the system’s best estimate of what is happening in the world and provides a compelling example of how even low-level sensory representations can be uncoupled from direct sensory stimulation. While the activity corresponding to the blind spot doesn’t directly respond to sensory cues in isolation, it is still a sensory representation in the sense discussed above, as it still serves to carry natural semantic information about what is happening in that region of the world, defeasible and interpolative as it is.

3.3 Motion Representation in Area MT

Unless we suffer from akinetotopsia, we don't see a series of disconnected snapshots of the world, but events unfolding smoothly in time (Schenk and Zihl 1997). Time is an ineliminable factor in motion perception: turn down the frame rate of a movie of water dripping, and the drips will appear to move more slowly, because the brain takes into account the temporal delays between frames. There is a certain window into the past within which the brain integrates sensory inputs to construct its estimate of what we are presently seeing.

In the primate brain, the motion-sensitive neurons in V1 project to a region known as area MT (Movshon and Newsome 1996). Single unit recordings have revealed that almost all of the neurons in MT are tuned to movement, with individual neurons showing strong preferences for stimuli that move in a certain direction (Albright 1984; Born and Bradley 2005). Just like the feature maps in V1, these neurons are topographically organized: neurons with similar motion preferences are clustered together into cortical columns (Fig. 3, from DeAngelis and Newsome 1999).

Activity in MT neurons is strongly correlated with behavioral performance on motion discrimination tasks (Newsome et al. 1989). Indeed, when MT activity is enhanced via cortical microstimulation at a single location, perceptual discrimination is altered in predictable ways: if the stimulated region contains neurons that prefer a certain direction of motion, monkeys are biased to respond as if stimuli are moving in that direction (Salzman et al. 1990, 1992). Further, if MT is chemically inactivated, performance on motion discrimination tasks is severely compromised,

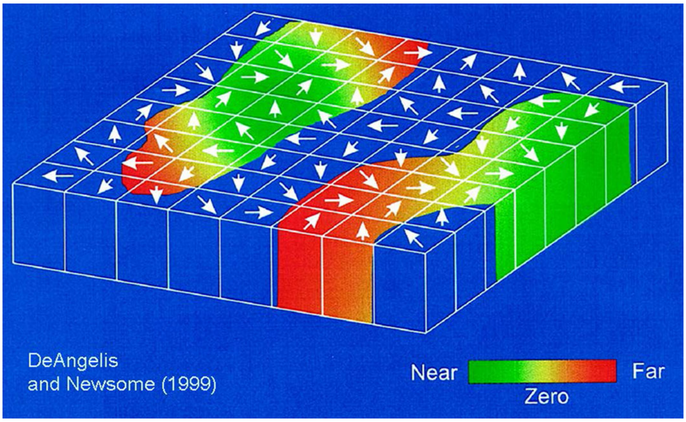

Fig. 3 Topographic representation of motion in monkey area MT. Each block indicates a cortical column that contains neurons tuned to motion in a particular direction. The colors represent neurons tuned to stereoscopic depth. (Reproduced with permission from DeAngelis and Newsome 1999)

while performance on other visual discrimination tasks remains unharmed (Newsome and Pare 1988).

Cumulatively, such data suggest that MT is not accidentally correlated with visual movement, but it's used by downstream networks that adaptively control behavior with respect to visual motion in the environment. That is, area MT contains a representation of visual motion, in the sense discussed in Sect. 2 (SR). Note we are not claiming that area MT *only* represents motion, or that motion representations are not learned: just as in V1, there seems to be multiplexed representation of many stimulus features (for instance, as shown in Fig. 3, it also represents depth. (For recent work on the plasticity of MT representations, see Liu and Pack 2017).

Area MT is just one of many higher-level visual regions: there are dozens in the primate brain, each specialized for processing different types of information (Felleman and Van Essen 1991). We could fill volumes telling the story of each such area.

Despite the relatively simple-sounding picture painted so far, the visual system does not process information in a strict feedforward hierarchical fashion. For instance, dense feedback connections are the norm, such as connections from MT to V1 (Maunsell and van Essen 1983; Rockland and Knutson 2000; Ungerleider and Desimone 1986). While such feedback is surely important (Gilbert and Li 2013; Hupe et al. 1998; Lamme et al. 1998; Muckli and Petro 2013), its exact function is uncertain and the subject of a great deal of speculation and active research.

Recently, the 'predictive processing' approach to sensory coding has gained popularity in neuroscience, but especially in philosophy and psychology. In that framework, one key function of top-down signals is to transmit sensory *predictions* to lower-level areas, while a key function of bottom-up signals is to transmit prediction errors (Clark 2016). We will remain neutral on predictive processing as well as most theoretical matters. Everything we say is compatible with their position: even the staunchest advocates of predictive processing would not dispute that *one* function of sensory systems is to carry information into the brain, since it is required to calculate sensory prediction error.

3.4 Illusions and Other Anomalous Perceptual Phenomena

It has been clear at least since Descartes that anomalous perceptual phenomena (hallucinations, dreams, illusions) are extremely difficult to explain if perception is just skilled engagement with the world, without any need for representational intermediaries (Noë 2010). This is most obvious when behavior is held fixed while perceptual content varies. Consider bistable perceptual phenomena such as the Necker cube or binocular rivalry, in which percepts alternate even if you do not change your response toward the stimulus (Fig. 4).

Why do such perceptual alternations happen? They occur because perceptual states toggle back and forth between two "interpretations" of the stimuli. We find that lower-level sensory representations, even in V1, track the perceptual states during the presentation of rivalrous stimuli like those in Fig. 4, and their representational contents match the perceptual contents: this has been observed

Fig. 4 Binocular rivalry demonstration. Project each image to a different eye (e.g., by placing a piece of paper perpendicular to the images), and fuse the checkered circles. Most people do not see a sum of the house and face, but rather the patterns alternate, seeing the house for a few seconds, and then the face for a while, and so on. This phenomenon is known as *binocular rivalry*. During transitions between percepts, the new percept will spread relatively quickly across the old as a kind of traveling wave. (Reproduced with permission from Tong et al. 1998)

using both single-unit recordings in monkeys, as well as fMRI in humans (Leopold and Logothetis 1996; Polonsky et al. 2000). For instance, when you perceive a red house, neurons tuned to the color red tend to be more active than neurons tuned to the color green.

As discussed in Sect. 2, we are not assuming that low-level sensory representations are sufficient for conscious experience. We are saying that sensory representations are *part* of a full explanation of perceptual phenomena, and that sensory representations offer resources unavailable if we restrict our explanatory base to behavioral criteria such as skilled engagement with the world. Such a restriction to events outside the skin would be an unprincipled explanatory straightjacket.

To sum up, nervous systems contain myriad sensory representational systems. Sensory representations have indicative content in the sense defined in SR, which means that they also guide behavior. For instance, if the visual map in V1 were suddenly inverted, we would expect an animal to become completely disoriented. Such disorientation is exactly what happens in sensory prosthetic systems when the spatial mapping from sensor to brain is scrambled after an animal has learned to use the prosthesis (Hartmann et al. 2016).

4 Uncoupled Representations

While sensory representational systems are prototypical, philosophers tend to be more interested in representations that are uncoupled from current sensory stimulation (Gardenfors 1996; Rouse 2015). This interest is likely due to curiosity about our ability to think about things that are not present to the senses, which underwrites much of our planning, counterfactual reasoning, and abstract thought (Gardenfors 2005).

Let's consider a few simple examples of uncoupled indicative representations. Like their coupled sensory analogues, these are activation patterns in the nervous system that carry information about the (possibly past) state of the environment as part of a broader mapping between internal and external states that guides action. Thus, these uncoupled representations fit (SR), our informational teleosemantic account of indicative representations. Note that there seem to be uncoupled imperative contents as well: in Sect. 5 we will discuss efference copy, or motor representations not directly causally connected to behavior.

4.1 Working Memory: From Receptive Fields to Memory Fields

Present a red square on a computer monitor, and then let the screen go blank for ten seconds. After this *delay period*, present a red square and a blue circle. A monkey or a person can reliably select the red square, indicating that they held information about the stimulus in memory during the delay period (Quintana et al. 1988). Monkeys are excellent at working memory tasks, in some cases significantly better than humans (Inoue and Matsuzawa 2007). While neuroscientists are still actively investigating the mechanisms underlying working memory tasks, a few key observations of the underlying mnemonic representations have emerged. We will focus on results from the prefrontal cortex, *PFC* (for excellent reviews, see Leavitt et al. 2017; Riley and Constantinidis 2016).

As demonstrated by multiple studies recording from single units during working memory tasks, a large percentage of neurons in the prefrontal cortex maintain a stimulus-specific representation of the target during the delay period (Fuster and Alexander 1971). Consider the classic *oculomotor delayed response* (ODR) task, which explores memory-guided saccades (Fig. 5a) (Funahashi et al. 1989; Takeda and Funahashi 2002). In the ODR task, the subject fixates on a central cue (such as a plus sign), and then a visual cue will briefly appear at a random location on the screen. After a delay period (usually between 1 and 40 s) the fixation point will disappear and the subject is rewarded for making a saccade to the location where the visual cue was presented.

A majority of individual neurons (recorded using single-unit extracellular recordings) in the PFC show sustained, stimulus-specific activity during the delay period. These mnemonic units have *memory fields*, an extension of the receptive field idea from sensory neuroscience: a memory field is the set of sensory cues that evoke a sustained response during the delay period (see Fig. 5b, from Funahashi et al. 1989). PFC neurons tend to be broadly spatially tuned, responding to stimuli in the contralateral visual field, just like neurons in lower-level sensory cortical areas like V1 (Takeda and Funahashi 2002).

One problem with the basic ODR task structure is that it cannot differentiate sustained activity that is mnemonic in nature from activity devoted to motor planning and execution. Does sustained activity in response to a cue represent the sensory cue or is it just used to generate the motor output, the saccade? To overcome such problems, which emerge when sensory and behavioral variables are so tightly coupled, researchers have come up with many clever variants of working memory

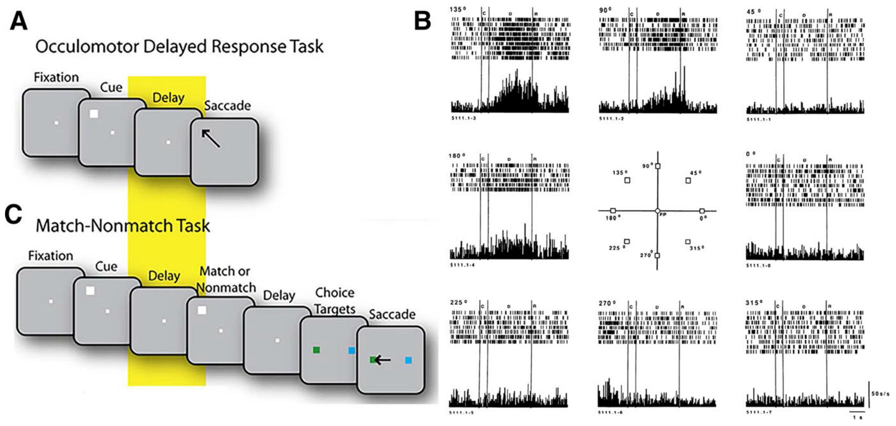

Fig. 5 Working memory: behavioral and neuronal perspectives. **a** Basic structure of ODR task described in the text. After fixation on a central spot, a visual cue appears at a random location on the screen. After a delay period of a few seconds, the fixation spot disappears, and the subject must saccade to the location of the original sensory cue to receive a reward. (Reproduced with permission from Riley and Constantinidis 2016). **b** Memory field in PFC neuron: the central graph shows the location of each possible saccade cue in the ADR, and the raster plots and PSTHs in the outer edge show the responses during the fixation, cue, delay, and saccade periods that were shown in panel A. (Reproduced with permission from Funahashi et al. 1989). **c** Schematic showing the match/non-match task structure. After fixation, a visual cue appears. After an initial delay period, a second visual cue appears, either at the same location (match) or a different location (non-match). Then, after a *second* delay period, two cues appear that contain information about where to saccade: toward the green square if the visual cues matched, and the blue square if they did not match. (Reproduced with permission from Riley and Constantinidis 2016)

tasks that tease apart sensory and motor components (reviewed in Riley and Constantinidis 2016). The majority of the neurons in PFC carry sensory signals.

For instance, when the intensity of the initial sensory cue is modulated—dim on some trials and bright on others—the sustained activity during the delay period is also modulated, with higher sustained responses to brighter stimuli (Funahashi et al. 1989). This suggests a sensory memory function, rather than a motor function, because the saccade amplitudes and trajectories are the same for the dim versus bright stimuli. More directly, in the delayed *anti-saccade* task, subjects saccade in the *opposite* direction of the initial visual cue on some trials, and in the same direction on other trials. This way, researchers can factor out which responses correlate with sensory cues, and which correlate with motor variables. The majority (59%) of individual neurons showed stimulus-selective memory effects, with 25% tuned to movement parameters (Funahashi et al. 1993). Similar results are seen in the ingenious *delayed choice* version of the task, called the *match/non-match* task (Fig. 5c). In this case, the subject initially doesn't know the appropriate saccade direction—information is only provided *after* the initial delay period (Qi et al. 2010).

Importantly, disrupting activity in the frontal cortex drastically impairs performance in delayed response tasks (Bauer and Fuster 1976; Funahashi et al. 1993; Fuster and Alexander 1970; Mishkin and Manning 1978). For instance, localized unilateral lesions to the prefrontal cortex produced significant deficits in the ODR task when the subject was required to saccade to locations contralateral to the site of ablation (Funahashi et al. 1993). Monkeys with such ablations were still able to perform *sensory-guided* saccades, in which the visual cue stayed present during the delay period (*ibid.*). This suggests the deleterious effects on the ODR task were based on disruptions of sensory cue processing and maintenance, rather than motor deficits per se.

Note we are not suggesting that PFC is a working memory *module*. The active maintenance of recent sensory events is not localized solely in the PFC, and the PFC has many other functions. On the first point, patterns of sustained activity during working memory tasks are distributed across multiple cortical and subcortical areas (Bolkan et al. 2017; Watanabe and Funahashi 2004), and the network mechanisms for generating this sustained activity are extremely active research topics (Murray et al. 2017; Wimmer et al. 2014; Zylberberg and Strowbridge 2017).

For instance, the posterior parietal cortex, which is involved in spatial attention and a key locus of visuospatial processing (Goodale and Milner 1992), has strong reciprocal connections to PFC. It also shows significant sustained activity during the delay period (Qi et al. 2010). However, there are asymmetries in their response properties, which suggests that PFC neurons tend to be more *directly* involved in maintaining task-specific information: for instance, the sustained activity in PFC neurons is relatively resistant to visual distractors presented during the delay period, while the sustained activity in parietal cortex is disrupted by such distractors (Qi et al. 2010). This has been replicated in other higher-level visual areas (Miller et al. 1996).

While the general story has held up quite well for some time, we will need additional behavioral experiments and simultaneous neuronal recordings from multiple areas to nail down the full story about the working memory system, in particular its relationship to its closely related cousin, attention (Gazzaley and Nobre 2012).

Note that well-crafted behavioral experiments, coupled with the general fact that maintenance of stimulus-specific information is required to solve working memory tasks, lets us infer that working memory is representational. In particular, the *data processing inequality* from information theory (Cover and Thomas 2006) is frequently used for "big picture", constraint-based thinking about how neuronal systems operate in a behavioral context, implicitly guiding a lot of back-of-the-napkin thinking in neuroscience. Roughly, this inequality states that if an animal's behavior carries information about a stimulus (e.g., which stimulus was presented a few seconds ago in a working memory tasks), then there must be internal states in the animal that carry *at least* as much information about the stimulus in the meantime.[4] It is no coincidence that among working memory researchers there is no significant debate about whether working memory involves representations; rather, debates and experiments are guided by the desire to discover the nature and distribution of the representations. *Inferring* representations from behavior and

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[4] Technically, the inequality states that if $X \rightarrow Y \rightarrow Z$ is a Markov Chain, then $I(X; Y) \geq I(X; Z)$, where I() is mutual information. Using this to theorize about internal states of the animal assumes that the behavior of the animal in the working memory task depends on some internal state of the animal after the stimulus was presented. This is easy enough to demonstrate by removing the brain of the animal.

generic informational considerations in this way is a useful, and relatively ubiquitous, first move toward representation *observed*.

4.2 Birdsong Learning: Memory-Guided Error Correction

Birdsong learning has long gone underappreciated among philosophers as a window into neural representation. It has proved to be an extremely fruitful model system for socially learned vocal communication, with many interesting parallels with human language evolution and acquisition (Bolhuis and Everaert 2013; Doupe and Kuhl 1999; Pfenning et al. 2014; Sereno 2014).

Birdsong learning happens in two main stages (Brainard and Doupe 2002; Mooney 2009). In the first, *sensory learning* stage, young songbirds listen to a conspecific tutor sing a song and acquire a memory of the song appropriate for its locale. In the next, *sensorimotor learning* stage, they finally start to sing and ultimately come to reproduce the tutor song that they heard during the sensory learning stage. Some songbird species go months between the sensory learning and sensorimotor learning stages, with no rehearsal during the intermission (Marler and Peters 1981). Where was the song between the two phases? Not in behavior. A *memory of the song* was stored in long-term memory.

While sensory learning happens quickly, sensorimotor learning is slow and requires vocal experimentation. At the beginning of the sensorimotor stage, birds emit rambling vocalizations similar to the babbling of human infants. Eventually they begin producing sections of song resembling those of the original tutor, and then slowly shape their vocalizations until they match the template stored in memory (Mooney 2009).

Sensory feedback is crucial during this sensorimotor learning stage. If a songbird is deafened before this phase, the animal never converges on the tutor song, but ends up producing distorted vocalizations that bear little resemblance to the tutor song (Konishi 1965). That is, songbirds undergo *feedback-guided error correction during the sensorimotor learning phase*. The error signal that guides learning is the difference between the song they produce and the memory of the tutor song (Mooney 2009).

While this is still an active area of research, a good deal of effort has been put into tracking down the representation of the tutor song (Hahnloser and Kotowicz 2010). There were breakthroughs on this in two recent studies of the swamp sparrow, a species that learns many different songs as juveniles in addition to the tutor song taught by its main tutor. Using extracellular recordings in a nucleus (HVC) known from ablation studies to be important for song learning and production, Richard Mooney's group found a population of neurons that selectively responds to songs in the adult bird's repertoire, but in particular contains stronger responses to its unique tutor song (Prather et al. 2010). In a follow-up study (Roberts et al. 2012), they discovered that disrupting activity in HVC (via optogenetic or electrical stimulation) prevents the acquisition of the tutor song.

4.3 Fetch! Recognition and Memory-Guided Search

Consider a dog looking for a ball, or waiting patiently for its owner as it sits on the front porch. This behavior suggests there exists an internal state guiding the behavior of the dog that allows it to recognize when the relevant condition is satisfied. While there are many technical arguments in the literature about object permanence in dogs (Miller et al. 2009), such arguments don't block the general point that dogs seek targets, and when they reach their target, their search ends in ways that are easy to identify. Dogs are like heat-seeking missiles when it comes to games of fetch. They can fetch tens, hundreds (Kaminski et al. 2004), and sometimes on the order of *a thousand* toys in a home *by name* (Pilley and Reid 2011).[5]

It is hard to come up with a plausible story about such goal-directed behaviors that does not involve some sort of internal representation of the target used by the dog, a *memory of the object* that explains the animal's ability to recognize when the target has been reached. This is much like the sensorimotor learning stage of birdsong, but on a much shorter time scale: the dog is comparing current sensory cues to an internal memory of the object for which they are searching. While an animal's behavior often provides the best evidence that an animal is searching (Ryle 1949), our *explanation* of such behavior will ultimately draw on facts about internal representations, in particular *memories of specific events* and *objects*.

Long-term memory stores are harder to observe and measure than occurrent sensory representations and working memories: long-term memories are not stored directly in ongoing electrical activity patterns in the brain, but latently in the long-term modifications of synaptic weights between neurons (Feldman 2012). Luckily for researchers, the study of long-term memory formation has been greatly helped by clues provided by neuropsychological patients. The most famous is HM who, after surgery for intractable epilepsy, began to suffer from severe anterograde amnesia. That is, he was unable to form new memories even though he retained memories from before the surgery. For instance, he could easily recognize faces of people he knew before the surgery, but not those he met after the surgery (Squire 2009). Interestingly, his disability was fairly specific to long-term memory: he had ordinary perceptual abilities, only slightly impaired language abilities, and in many other ways he seemed normal (Skotko et al. 2005). He could even acquire new motor skills like learning to ride a bicycle or using a new tool, even though he could not consciously remember going through the process of learning them (Shadmehr et al. 1998).

The discovery of such syndromes was a watershed in the study of memory formation across the animal kingdom (Kandel 2006; Squire and Wixted 2015; Squire et al. 2004). It suggested that, in mammals, the hippocampal formation is important for formation and consolidation of long-term memories, but that extra-hippocampal regions (such as the cerebral cortex) are the long-term storage houses

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[5] Note that humans beat dogs by a good order of magnitude. One study presented 10,000 pictures to passive observers in one sitting, and they were later able to recognize them with 90% accuracy (Standing 1973).

for such memories. This view has held up to more rigorous tests in model systems (Kitamura et al. 2017; Morris et al. 1982; Nabavi et al. 2014; Whitlock et al. 2006). For instance, activity-dependent cell labeling is a recently developed technique that allows researchers to selectively stimulate neurons that are active in a given context (e.g., a room with specific visual cues) (Reijmers et al. 2007). In a recent "false memory implant" paradigm, researchers used this technology to genetically tag a group of cells active in a certain chamber; and then they used optogenetic stimulation on these same neurons, but paired this stimulation with a foot shock, which evokes a behavioral "freezing" response. Later, when introduced back to the original chamber, the animals exhibited a freezing response, even though they had never actually been shocked in that room (Ramirez et al. 2013).

5 Motor Representations

While sensory representations carry information from the world into the brain, motor representations have a different role: they function as commands: instructions sent from the brain telling the body where to move in the world.

Whereas the experimental study of sensory representations typically involves observing neuronal responses to different stimuli, the study of motor processes is often quite different. Since the motor system is sending *commands* to the body to move, one mainstay in the study of motor control is the artificial generation of movements via the electrical stimulation of the motor regions of the nervous system. Neuroscientists then assign content to motor representations by observing the resultant patterns of muscle contractions, movements, and adjustments of the external environment. This is in line with (MR), our teleosemantic account of the semantic content of imperative representations.

While the content of some sensory representations is potentially phenomenologically available, the same is not obviously true of motor representations. However, when gross *disorders* of the motor system emerge, the results are usually obvious to everyone. Errors in motor systems involve a breakdown either in the production, or readout, of commands sent to the body to move. In extreme cases, such as Tourette's syndrome or hemiballismus, the body engages in large-scale involuntary behaviors such as flailing or vocalizations. In cases of peripheral nerve deficits, such as spinal paralysis or Lou Gehrig's disease, intentions to move are still produced centrally, but not extracted appropriately by the downstream circuits that normally control behavior (Truccolo et al. 2008).

Let's consider some examples of motor representations, from motor maps to efference copies, and finally end with a brief discussion of *mixed* representations, which have both indicative and imperative content.

5.1 Motor Maps: From Homunculi to Ethological Action Maps

In the primate brain, the primary motor cortex (M1) is part of a large collection of regions that act together to control movement. If you briefly stimulate a small region of tissue in M1, you will typically produce a localized muscle twitch in response.

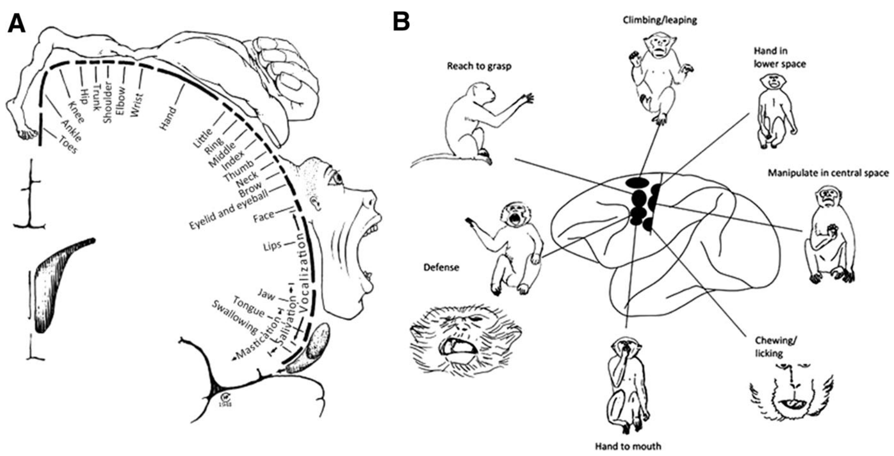

Fig. 6 From muscles to action maps. **a** Traditional motor homunculus, showing where muscles twitch when (human) M1 is briefly electrically stimulated. **b** Ethological action maps show the clusters of action types evoked by longer trains of electrical stimulation delivered to M1 in unrestrained monkeys. (Both panels reproduced with permission from Graziano 2016)

Based on such studies, a somatotopic map of the motor representation in M1 can be built, a motor homunculus (Fig. 6a) (Penfield and Boldrey 1937). These somatotopic maps are analogous to the retinotopic maps we met on the sensory side (Fig. 2). When a particular region in the homunculus is damaged, animals, including humans, typically experience immediate deleterious side effects in the form of paresis—an impairment in voluntary control that includes partial paralysis and loss of fine motor-control—in the corresponding body part (Darling et al. 2011).[6]

When researchers provide stimulation trains on ethologically relevant time scales (around half a second) and do not restrict animal movement, the picture that emerges is radically changed. Instead of individual muscle twitches, what are typically observed are ethologically meaningful behavioral patterns involving coordinated activity among multiple muscle groups. These actions include taking defensive postures, moving the hand toward the mouth, or reaching the hand forward as if to grasp an object (Fig. 6b) (Graziano et al. 2002). Such ethological action maps have now been observed in microstimulation studies in multiple primate and rodent species (Graziano 2016).

While stimulation studies are very informative, they are somewhat artificial. The brain doesn't work by indiscriminately shocking localized voxels in the cortex, or individual neurons (Brecht et al. 2004). Real motor control is more subtle and

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[6] Note that ablating M1 does not always lead to *permanent* paresis, but more short-lived and subtle motor deficits (Schwartzman 1978). Sometimes such ablations show no notable motor deficits, but instead deficits in motor *learning* (Kawai et al. 2015, though see Castro 1972; Makino et al. 2017). Such results undermine simple stories in which M1 is the final common output driving all movement. Some of the most recalcitrant movement deficits such as Parkinson's disease result from damage to subcortical structures like the basal ganglia. As discussed briefly at the end of this section, motor control is distributed across multiple cortical and subcortical areas, and the focus on M1 here is a convenience meant to keep the discussion contained, not an endorsement of strict localizationist theories of M1 motor control.

complex, with commands broadly distributed across a diverse collection of cortical areas, subcortical nuclei, and the cerebellum (Hewitt et al. 2011; Houk and Wise 1995; Shadmehr and Krakauer 2008). To examine the representations that the *brain* (as opposed to experimenters) generates, we must observe how the brain's activity naturally unfolds as animals engage with the world in real time.

5.2 Receptive Field Envy: Movement Fields, Force Fields, Goal Fields?

If you were to observe the activity in the brain of a monkey moving about in the world, you would notice that neuronal activity in M1 precedes movement of its body in highly reproducible ways. For instance, before the monkey moves its hand, there is elevated activity in its hand representation in M1 about 100 ms before the movement actually starts (Kakei et al. 1999). Indeed, the cortex is such a reliable indicator of future movement that some of the most promising clinical work lies in extracting intended movements from activity in the motor cortex of paralyzed patients, and then using such signals to control prosthetic limbs (Alexander and Crutcher 1990; Ganguly and Carmena 2009; Hochberg et al. 2012; Truccolo et al. 2008).

What shape do motor representations take in M1? This is a very active area of research, but there are a few results with which everyone should be familiar. In one classic study, researchers trained monkeys to move their hands in one of eight directions while recording from individual neurons. Similar to the movement-sensitive sensory neurons in area MT, neurons in M1 showed pronounced *direction tuning*. That is, they fired more action potentials before the monkeys moved their hands in a particular direction (Fig. 7: Georgopoulos et al. 1982). This led to the emergence of the concept of a *movement field* for M1 neurons.

It turns out that movement direction is just one of many features to which individual neurons in M1 are tuned. There have been extremely vigorous debates in the literature about whether M1 neurons are better described as tuned to velocity, force, activity in individual muscles, muscle synergies, or goal-directed acts such as grasping small objects (Chang et al. 1947; Georgopoulos and Ashe 2000; Griffin et al. 2015; Holdefer and Miller 2002; Kakei et al. 1999; Moran and Schwartz 2000; Scott 2000; Todorov 2000a, b, c; Umilta et al. 2008). Populations of neurons in M1 appear to represent all of these different (and often highly correlated) variables in flexible ways that can change rapidly with task context, posture, and learning (for an excellent review, see Kalaska 2009).

It seems that the same neuron does not always encode a single parameter, but can be recruited to help produce different behaviors in different contexts, such as when an external force is applied to the arm (Li et al. 2001), and the same neuron will produce different activity patterns when the animal is preparing to move versus actually moving (Elsayed et al. 2016).

There have been many recent debates about M1 representations, with two main axes along which opinions have tended to diverge: the kinetic/kinematic axis, and the implicit/explicit axis (Fig. 8). We have already implicitly discussed the first, *kinetics/kinematics*, axis. Briefly, this is about whether M1 neurons encode high-level kinematic features of movement such as velocity and position (Georgopoulos

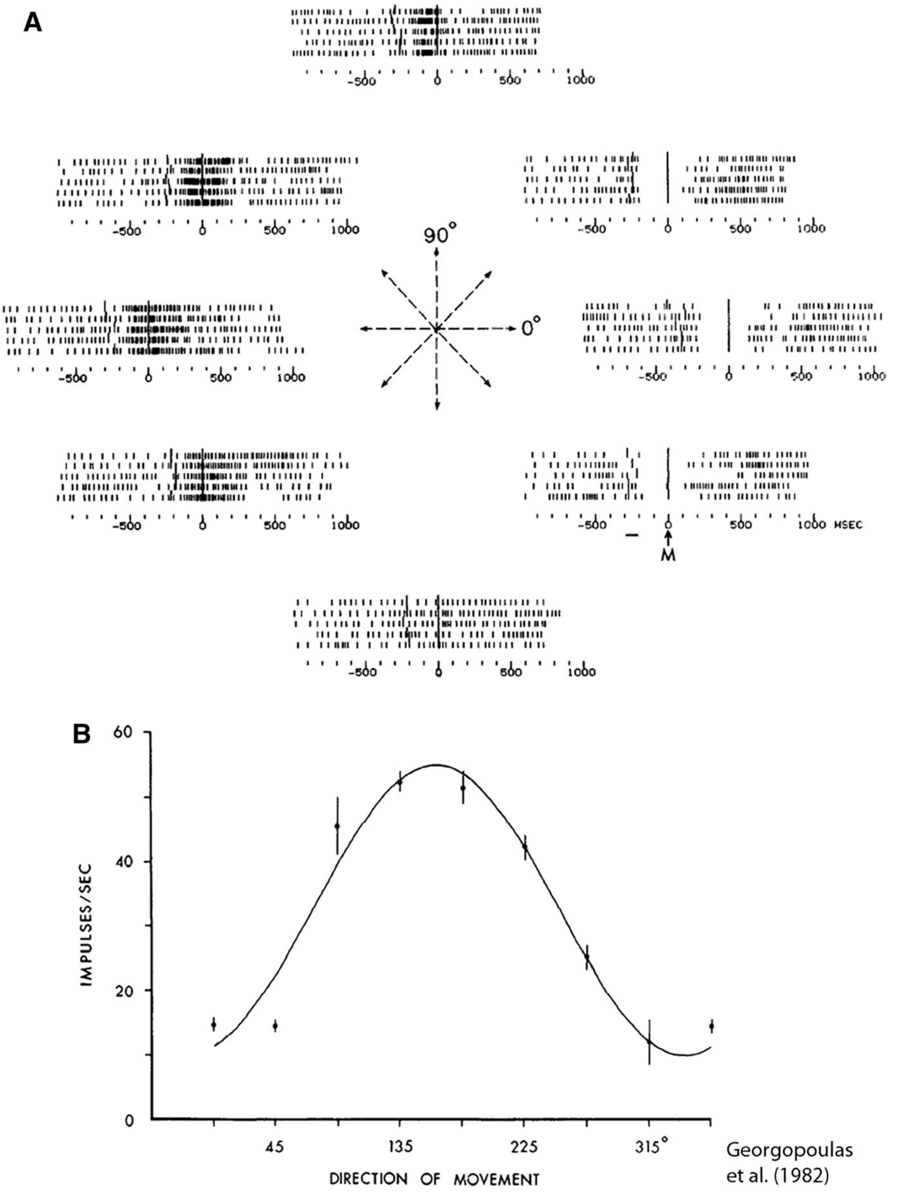

Fig. 7 Movement field in M1. **a** Response of a neuron in M1 to hand movements in eight different directions. Response is displayed as a raster plot for each direction. A raster plot shows a different trial on each row, with individual action potentials as tic marks. (Reproduced with permission from Georgopoulos et al. 1982). **b** Movement field shows the mean number of spikes as a function of the direction in which the monkey moved its hand. This neuron preferred leftward movement. *Ibid*

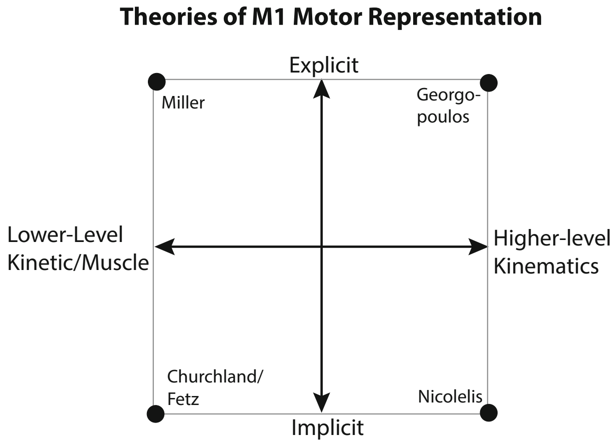

Fig. 8 Space of M1 representational theories. Debates about M1 representational structure have centered around where in this space M1 representations best fit. See text for details

et al. 1982, 1986; Wessberg et al. 2000), or low-level kinetic factors that cause movements, such as muscle forces or electrical activity in muscle fibers (Holdefer and Miller 2002; Sussillo et al. 2015).

On the implicit/explicit front, many researchers have argued that there are no fixed parameters encoded by individual M1 neurons (Fetz 1992; Pruszynski et al. 2014; Sussillo et al. 2015). Rather, it is entire *populations* of M1 neurons that encode such parameters, in such a way that the experimenter (or downstream consumer networks that actually control behavior) must extract the relevant parameters from such activity.

Implicit coding is a quantitative notion, such that a neuronal population *implicitly* represents some feature proportional to the computational cost required to extract information about that feature (Kirsh 2006). ‘Computational cost’ is typically cashed out in terms of the types of computations that neural networks can easily perform, such as taking weighted sums (Koch 2004), or linear classification (Rust 2014).[7] This analysis makes intuitive sense: if someone merely *implies* something, this suggests there is a cognitive cost incurred in *extracting* the implied content. The idea is the same here. For instance, if there is a face in your visual field, there is an implicit representation of a face in your retinal ganglion cells because it would require a great number of computational steps to extract this information. Compare this to visual area IT in monkeys, which has individual neurons that fire like crazy when faces are present (Chang and Tsao 2017; Perrett et al. 1982). These provide explicit representations of faces, because the computational cost required to extract the information that there is a face present in the visual field is relatively low.

For the past few decades, we have seen this distinction playing out in arguments about how M1 represents movement (Fetz 1992). For instance, in Georgopoulos’

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[7] Discussions of explicit/implicit coding have always taken place in the sensory system, so it is not actually clear if these are the correct standards to use for M1, which tends to send its outputs to muscles and central pattern generators (Kalaska 2009).

framework, velocity is explicitly coded in the firing rate in M1 neurons (recall Fig. 7).[8] On the other hand, other researchers have suggested that information about movement is not reliably coded in individual M1 neurons, and to extract the intended movement based on M1 activity requires relatively sophisticated decoding algorithms applied to large populations of M1 neurons, often taking into account their dynamical (time-dependent) nature. This can be found in the work of Nicolelis (Wessberg et al. 2000), as well as more recent work from Mark Churchland (Sussillo et al. 2015). In practice most people are not extreme advocates of either pole, falling somewhere in the middle in Fig. 8 [e.g., you can find elements of both types of codes discussed in Wessberg et al. (2000)].

Presumably, those who think M1 only encodes movement implicitly would say that the downstream spinal networks that control behavior must "extract" the information implicitly contained in the M1 commands, and generate the appropriate movement sequences, such as walking, based on such commands. This is not at all far-fetched. In fact, it is sort of the standard model of motor control: it has been known for over a century that spinal networks contain central pattern generators and sensory-feedback mechanisms that allow mammals to carry out extremely complex motor trajectories like walking even when the cerebral cortex has been completely severed from the spinal cord (Rossignol and Bouyer 2004; Sherrington 1910).

Recently, Mark Churchland has putatively been arguing for a nonrepresentationalist account of M1 function. Specifically, he has been arguing against the existence of traditional velocity-tuned neurons, and focused on the heterogeneous and dynamical nature of populations of M1 neurons in the direct control of movement (Churchland et al. 2010; Sussillo et al. 2015). However, when you dig deeper, his work seems to fall cleanly into the implicit/kinetic corner of the representational space in Fig. 8. That is, his research seems to be pushing against *a species of* representational theory, rather than representations *tout court*. Indeed, in a recent modeling paper they say, "[A]lthough *the model certainly contains an implicit representation of the upcoming EMG*, individual-neuron responses rarely match the patterns of EMG" (Sussillo et al. 2015, p. 1032, emphasis added). Note EMG is a measure of electrical activity in muscles, so this falls into the kinetic side of the representational landscape.

Note that if M1 representations are indeed implicit, one implication is that researchers will need to record activity from populations of neurons in order to faithfully reconstruct the representational content of the activity. It is likely no coincidence that, as multielectrode recording techniques have become more prevalent, the importance of implicit coding in M1 and other areas has become clearer.

It is important to note that M1 does not represent movement simply because its activity occurs *before*, or *causes* movement. If that were the case, then even electrical activity in muscle fibers would represent movement. Interestingly, just as individual photoreceptors are not described in (sensory) representational terms,

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[8] Note that 'implicit' is not the same as 'distributed' or 'population' code. 'Implicit' implies 'population' but not vice versa. Even in Georgopoulos' work, perhaps the *locus classicus* of explicit motor representations, to know the velocity of the animal's arm you must know the firing rate of the population of M1 neurons. That is, everyone in the game accepts that motor control involves a distributed code.

muscles are *never* described in (motor) representational terms. This may seem a trivial point, but the transform from electrical activity in muscle fibers to bodily motion is quite complicated—electrical activity in muscles causes muscle shortening via complex biochemical cascades; the forces generated are filtered through the springs and masses of the musculoskeletal system, and are strongly influenced by what the other muscles in the body are doing (Buchanan et al. 2004; Lloyd and Besier 2003).

That is, *despite* the time delays and inherent complexity involved in the transform from muscle activity to movement, muscles are not representational. Instead, motor representations take the shape of an ongoing superposition of more basic, centrally generated, behavioral commands. The particular superposition produced at a given moment depends on the current goals of the organism, sensory information, and recent movements. It is *this ongoing, goal-directed command, and its construction, that is representational*—not electrical activity in muscle fibers. Muscles and bones "consume" motor representations—they are *part of the body* and the ultimate recipients of motor commands. After all, as discussed above, you can have active intentions to move without overt movement, as in cases of paralysis or other disorders of motor control.

In general, in both sensory and motor representational systems, it is standard to quantify the *accuracy* of the system (or, inversely, its error level). In motor systems, this accuracy is quantified in terms of closeness to the goal (e.g., did the eye saccade to the target, did the hand reach the apple). In sensory systems, it is in terms of how accurately you can reconstruct the stimulus, given the neuronal response (Bialek and Rieke 1992; Thomson and Kristan 2005). These two error measures conform to the different representational functions of motor and sensory systems, respectively.

It is in virtue of the goal of a motor command that we can assign an error measure to the command, and track this error to multiple sources. It could be representational (e.g., in Tourette's syndrome, which seems to be partly due to unintended disinhibition of basic motor commands in the basal ganglia), or have to do with faulty readout of the command, which can be quite drastic (e.g., spinal cord damage), or commonplace (e.g., you cannot lift that barbell because of muscle fatigue). In the case of muscle fatigue, the failure is due to the readout mechanisms of your commands, much like you could see a shape incorrectly when seen through a distorting lens (the sensory analog of Tourette's would be a centrally generated visual hallucination).

5.3 From Efference Copy to Sensory Cancellation

When the brain sends commands to the body to move, *the brain sometimes signals to other parts of the brain that it has sent this command.* In the literature, these signals are called *corollary discharge*, or *efference copies*.[9] Evidence is growing

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[9] Sometimes these terms are used differently. For instance, 'corollary discharge' is sometimes taken to be the output of a forward model (see below). However, the two terms are typically used as synonyms in the literature. For instance, "A ubiquitous strategy is to route copies of movement commands to sensory structures. These signals, which are referred to as corollary discharge (CD), influence sensory processing in myriad ways" (Crapse and Sommer 2008). It would be a mistake to conclude, as (Clark 2016) does,

that efference copy is important in both sensory perception and motor control (Crapse and Sommer 2008; Wolpert and Miall 1996). Let's consider its role in each process. One reason that efference copy bears emphasis is that some theorists have expressed skepticism about its existence (Clark 2016).

The clearest *intuitive* evidence that corollary discharge is important in perception comes from the eye movement system (Collins 2010). When you voluntarily move your eyes via the rapid, ballistic eye movements known as *saccades*, the world doesn't seem to jump about erratically. However, if you poke your eye (gently) with your finger, the world *does* appear to jump. When you perform saccades, the retinal motion is actually much larger than when you poke your eye with your finger, but somehow the world looks relatively stable. These phenomena suggest that the visual system uses efference copies generated by your eye-movement system to "subtract out" the sensory consequences of eye movement, a phenomenon known as *saccadic suppression* (McFarland et al. 2015).

In general, it is often important for animals across the phylogenetic spectrum to keep track of which sensory responses are self-generated and which have other causes. There is evidence of efference copy from multiple sensory systems in multiple phyla (for an excellent review, see Crapse and Sommer 2008). We will consider a few examples here, starting with the superior colliculus in the eye movement system.

The superior colliculus (SC) is a complex multi-layered brainstem nucleus that is involved in visual selective attention and orienting responses, including saccades (Krauzlis et al. 2013). Neurons in its superficial layers are visually responsive, displaying keen motion sensitivity. Unlike neurons in area MT (Sect. 3.3), most SC neurons are 'pandirectional', preferring no particular direction: they simply fire when something is moving at a particular location in space (Goldberg and Wurtz 1972). Neurons in the deeper layers contain a (motor) representation of saccade direction and velocity, and exhibit classical movement fields (as in Sect. 5.2). If you stimulate deep-layer SC you will generate saccades or even whole-body orienting toward stimuli; ablation of deep SC layers disrupts saccades (Gandhi and Katnani 2011; Sparks et al. 1990). It has been suggested that the superficial visual layers of SC form a kind of 'salience map' of the visual field, and that there is a sensorimotor transformation from superficial to deep SC, with the latter generating orienting responses to the salient stimuli represented in the superficial layers (Kustov and Robinson 1996; White et al. 2017).

The problem animals face is that it would be maladaptive to constantly sense salient motion that they have generated *by moving their own eyes*: this would be a constant source of distraction if the goal was to use the SC to orient toward stimuli moving in the environment. The solution to this problem is powerful saccadic suppression in the superficial layers of the SC (Robinson and Wurtz 1976). That is, the same moving stimulus that would generate a large response in superficial SC

Footnote 9 continued
that a paper doesn't support the existence of efference copy just because it uses the phrase 'corollary discharge'.

generates no response to identical visual inputs generated by self-generated saccades.

There are a few reasons to think this extra-retinal SC suppression is generated by efference copy rather than sensory inputs generated by eye movements (such as proprioception). One, even in complete darkness, superficial SC baseline activity is suppressed during saccades (Robinson and Wurtz 1976), which suggests the suppression is not generated by visual stimuli. Two, freezing eye movements by paralyzing the eye muscles in animals that are still sending out saccade motor commands still generate saccadic suppression (Richmond and Wurtz 1980). This suggests such saccadic suppression is not generated by proprioception or actual movement, but *intended* movement. Third, recent anatomical analysis of SC circuits, single-unit recordings in brain slices revealed that deep SC neurons send out an axonal arbor that loops back to excite superficial SC inhibitory interneurons, providing a basis for the efference copy, along with a mechanistic account of saccadic suppression (Phongphanphanee et al. 2011).

Efference copy is not confined to vision, or mammals. In the cricket, there is a single interneuron, aptly named the 'corollary discharge interneuron' (Poulet and Hedwig 2006) that responds to the central-pattern generator that produces the leg movements responsible for their chirps. This interneuron exerts enough inhibitory control on auditory neurons to filter out its own auditory signals, but the cricket can still respond to externally generated auditory cues (Poulet and Hedwig 2003).

Note that efference copy and its resultant sensory compensation do not always produce generic suppressive responses (Confais et al. 2017). One interesting case comes from weakly electric fish of the family Mormyridae (Bullock 1982). Such fish contain an electric organ that periodically generates an electromagnetic (EM) field, an *electric organ discharge* (*EOD*): electric fish use the resulting distortion of the local EM field to sense objects in its environment (Heiligenberg and Bastian 1984; Krahe and Maler 2014). How do the mormyrids differentiate self- and environmentally-generated changes in EM fields? The efference copy mechanism has been worked out relatively well (Bell et al. 1983; Carlson 2002). Interestingly, in the brain region that processes the response to the EOD, efference copy doesn't produce some generic suppressive effect, but a *negative image* of the sensory consequences of the EOD, a negative image that cancels out the response usually produced by the animal's EOD (Bell 1981). Figure 9 is a schematic depiction of this sensory cancellation process.

What if you artificially *distort* the EM field in the animal's environment after every EOD? Amazingly, within minutes, they acquire the ability to cancel such artificially generated EM fields. In other words, the electrosensory system rapidly learns to cancel out novel sensory consequences of its EOD, seeming to interpret the predictable EM field as a self-generated environmental perturbation whose consequences need to be filtered out during its search for externally generated sources of change (Bastian 1996; Bell 1982). This is now one of the better-studied

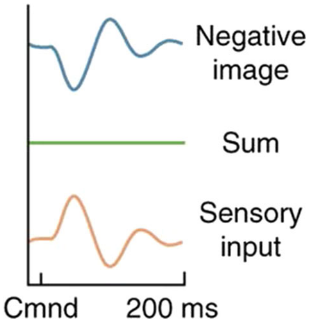

Fig. 9 Sensory cancellation in weak electric fish. Cartoon representation of input to sensory neuron in the PLL in mormyrid. The sensory input comes in from the ampullary electrosensory system, the negative image is generated via processes downstream from the command nucleas that triggers the EOD. The two signals converge in cells in the PLL, cancelling each other. (Reproduced with permission from Kennedy et al. 2014)

instances of efference copy and sensory suppression, and has been studied in depth at the cellular level (Kennedy et al. 2014).[10]

There is a paradoxical feature to efference copy: it does not directly control behavior, but we are calling it a motor representation. When a motor representation is copied to auxiliary areas to influence processing, we consider them efference copies that inherit the imperative representational content of their sources.

5.4 Efference Copy in Motor Control: Forward Models

Efference copy is not only important for sensory processing. It is integral to what has become one of the main models of voluntary motor control. This involves the construction of *forward models that predict the sensory consequences of particular behaviors*. The following summary will necessarily be brief (for more detailed reviews, see Shadmehr et al. 2010; Wolpert and Miall 1996).

When moving around in the world, we do not passively respond to incoming sensory inputs such as the weight of a heavy box we are lifting. Our brain builds up expectations and predictions about what is going to happen, and uses those predictions, coupled with our goals, to shape our behavior *before* those consequences can happen. We brace ourselves *before* picking up heavy objects. We prepare our bodies to catch balls well before the ball arrives (Lacquaniti et al. 1992). There is growing evidence that such predictive anticipatory processes are actually knitted into basic low-level motor control mechanisms.

Let's consider a concrete example. When you are shaking a saltshaker, you do not grip it with the exact same force the whole time. Rather, you typically unconsciously change your grip force in ways that *anticipate* the changes in torque

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[10] Why would such plasticity be useful in the electric fish? The local EM fields produced by the same EOD can change depending on changes in water resistivity, or if the animal is swimming, or spending considerable time next to a nonconducting surface such as a rock or air at the water's surface (Bell 1982), so the sensory consequences of the EOD are likely malleable enough that it is helpful to learn them (Bell 1981).

and load force that will be exerted against your hand, so that the saltshaker will not fall out of your hand. Your grip increases to compensate for changes in the frictional forces at key times, such as when you jerk the shaker at the bottom of its trajectory and is most likely to slip out of your hand (Johansson and Cole 1992).

Obviously, the motor commands coming from the motor system are sent *before* muscle contraction. Hence, the increase in grip forces that are synchronized to load force changes cannot be happening in response to sensory feedback: our motor control machinery is somehow *anticipating* what is going to happen. For that matter, people will often change their grip *before* the relevant environmental events even occur: for instance, people will increase grip force just *prior* to lifting an object (Forssberg et al. 1992). Thus, adjusting motor commands to anticipated changes requires memory of previous interactions with objects (Johansson and Cole 1992).

Evidence has started to converge that the brain accomplishes this feat using internal feedback loops that predict sensory feedback, also known as forward models. In the simplified model in Fig. 10, the motor controller generates a motor command to directly control behavior (e.g., from M1 to the spinal cord). But this motor command also branches off into an efference copy that is delivered to a system that contains a model of the controlled domain, and predicts the sensory consequences of the behavior that will result from the command. This system, which receives efference copies and predicts sensory consequences, is known as a *forward model*. The function of the forward model is to *predict the sensory consequences of that motor command*. That is, what sensory feedback will this action create? In this case of gripping an object, what tactile responses will the saltshaker produce: in particular will it slip? If so, go ahead and create the appropriate changes in grip strength *before* that deleterious consequence actually happens.

We have already implicitly discussed one forward model in the weakly electric fish. There the motor command was the same every time: ‘Produce an EOD’. When shaking a salt shaker, the motor command will continuously vary over time. However, if the internal model is accurate, it will predict the sensory feedback that will be generated by your behavior with the particular object you are using. As suggested by the red loop in Fig. 10, calculating this sensory prediction will also take some time, but the point of the forward model is that it produces internal feedback significantly faster than *actual* sensory feedback from the body, so the motor controller can beat it to the punch (Wolpert and Miall 1996).

We have left out many details. One, how is the forward model supposed to be acquired and updated? As you might guess, this would involve tuning model parameters based on sensory prediction error: the difference between actual feedback and predicted feedback (Shadmehr et al. 2010). We also left out discussions of how predicted sensory feedback is combined with *actual* sensory feedback during online motor control—after all, if you are shaking a salt shaker, and feel it starting to slip out of your hand, you will not just keep on going as if nothing is happening (Scott 2016). Third, how detailed is the internal model: does it contain explicit representations of the body and environment, or does it construct simple lookup tables, something just simple enough to help an animal get by, like in the electric fish? There are reasons to think that the models are more generalizable than

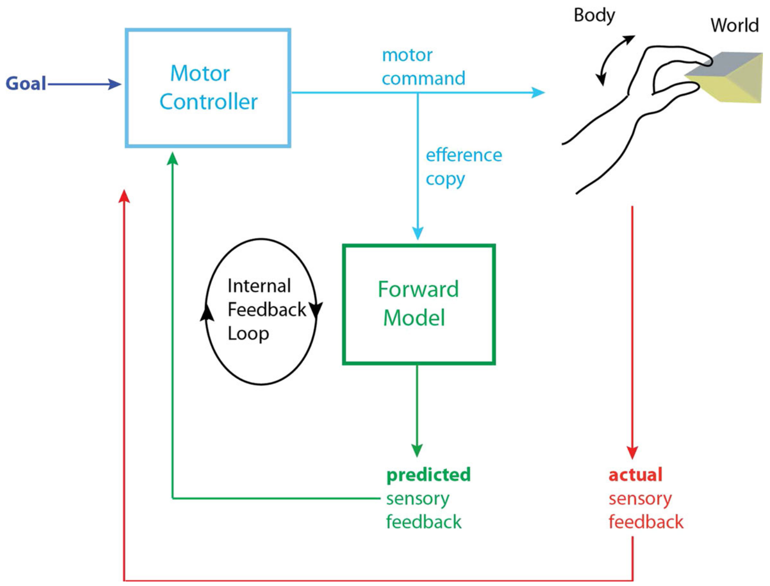

Fig. 10 Forward models and efference copy. Cartoon representation of the use of forward models for anticipatory motor control. See text for details. Forward models use efference copies of the motor command to predict the sensory consequences of that motor command, generating internal predictions that can be used by the motor control systems to generate appropriate behaviors before those sensory consequences actually happen

that, and show nuanced sensitivity to physical and dynamical features of the body and manipulanda (Lisberger 2009).

Stepping back from its theoretical virtues, is there *evidence* that forward models actually exist, that they are instantiated in brains? Early on, much of the evidence for these models was behavioral, or based on engineering or mathematical considerations (Volkinshtein and Meir 2011). But in neuroscience the armchair isn't good enough: we have to do the experiments. Initially, because of its intrinsic anatomical structure and connectivity patterns with the rest of the brain, and the fact that damage to this region impaired feedback-guided motor control, the *cerebellum* was the prime suspect to be involved in many of the operations attributed to the forward model (Ito 1970; Wolpert et al. 1998).

Decades have passed since Ito first posited forward models in the cerebellum, and there has been an ongoing confluence of theory and experiment, with many studies confirming that the cerebellum is indeed a locus of many expected features of forward models:

- The cerebellum directly receives efference copies. For instance, researchers showed that a population of spinal neurons crucial for motor control also sends collateral axonal branches to a cerebellar input nucleus, effectively sending an efference copy from the spinal cord up to the cerebellum. Then, using optogenetics, they silenced this efferent branch, and the animal's reaching behavior was severely compromised, thereby showing the importance of this efferent copy in active motor control (Azim et al. 2014).

- The cerebellum generates predictions of sensory consequences, which are the expected output of forward models. Researchers showed that one lobe of the cerebellum contains sensory predictions about visual stimuli: namely, visually responsive neurons do not just respond to actual visual stimuli but *expected* visual responses during a visual tracking task in cats, even when visual stimuli were temporarily shut off during the task (Cerminara et al. 2009). This suggests that the cerebellum is not just involved in active sensory representation, but in sensory *prediction*.
- The cerebellum contains sensory prediction errors, which are required for sculpting forward models. A recent study used extracellular recordings of single units in monkeys, and showed that neurons in an output nucleus of the cerebellum track sensory prediction error, or the discrepancy between predicted and actual sensory feedback (Brooks et al. 2015).

While we have come a long way in our study of forward models, there is still a long way to go. The cerebellum is an extremely complex, variegated structure, containing at least three times as many neurons as the cerebral cortex (Herculano-Houzel 2010). So far, the handshake between theory and experiment has been very promising.

It is natural for people to view the forward model as a kind of simulation or emulation of the world and its dynamics, a simulation uncoupled from sensory inputs (Grush 2004). Hence, this framework is sometimes extended well past its original domain of motor control, and figures prominently in more general philosophical theories of the mind (Grush 2004; Pickering and Clark 2014). Given the current pace of experimental investigations, we expect that within 20 years we will have a much better empirical handle on the appropriate scope of forward models. What behaviors and neuronal processes will be fruitfully illuminated by these models developed to explain why we grip the salt shaker at exactly the right time?

5.5 Mixed Representations

Another type of sensorimotor processing involves *sensorimotor transformations*, in which sensory representations are quickly and directly converted into motor commands (Lewis and Kristan 1998a; Salinas and Abbott 1995). This is what happens when the frog flicks its tongue toward the fly, or you saccade to where a bright light appears in your visual field. Such sensorimotor transforms often involve individual neurons, and neuronal populations, that are simultaneously sensory and motor representations. In other words, despite all the distinctions above, we do not mean to suggest that there are segregated sensory and motor modules in the nervous system. We have been making *conceptual* distinctions that are often not honored in real brains (Cisek and Kalaska 2010; Matyas et al. 2010).

6 Conclusion

We have briefly reviewed a small but representative sample of empirical findings about neural representations. Sensory and uncoupled representations form maps that guide behavior based on the information they carry, whereas motor representations also form maps that guide behavior to accomplish what they represent; thus, the functional role and explanatory power of neural representations depends on their semantic content.

While much empirical and conceptual work is still needed to fully understand neural representations and all that they can explain, one conclusion is safe. Using a variety of methods, neuroscientists have empirically discovered that some of the complex neural states interleaved between behavior and their environments are representations. Neural representations are observable, quantifiable, manipulable, and have received multiple independent lines of empirical support. Therefore, neural representations are real—as real as neurons, action potentials, and other entities routinely observed and manipulated in the laboratory.

Once we recognize that neural representations are real because they are routinely observed and manipulated experimentally, the long-standing debate over representations should finally be settled. Representations are no longer mere theoretical posits: they are as established a part of our ontology as anything that can be empirically discovered.

One corollary is that representing the world does not depend on linguistic behavior or related social practices (contra, e.g., Brandom 1994, pp. 69ff). The vast majority of our examples are from non-human animals and involve neither language acquisition nor language use or other types of social communication. Language itself cannot emerge *ex nihilo*: its evolution and development depend on the kind of primordial neuronal representational systems we discussed above (a point also made in Sellars 1981). There is nothing wrong with the *methodological* decision to gloss over such details and tackle higher-level questions about the cognitive significance of language. But even *if* we could read some semantic contents directly off of discursive practices, without any consideration of underlying mechanism, this would not undermine the existence of prelinguistic neural representational systems and the crucial role they play to enable those very discursive practices.

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References

Adams, F., & Aizawa, K. (2010). Causal theories of mental content. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy* (Spring 2010 Edition). https://plato.stanford.edu/archives/spr2010/entries/content-causal/.

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology, 52*(6), 1106–1130.

Alexander, G. E., & Crutcher, M. D. (1990). Preparation for movement: Neural representations of intended direction in three motor areas of the monkey. *Journal of Neurophysiology, 64*(1), 133–150.

Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience, 20,* 303–330. https://doi.org/10.1146/annurev.neuro.20.1.303.

Anscombe, E. (1957). *Intention*. Ithaca, NY: Cornell University Press.

Armstrong, D. M. (1973). *Belief, truth, and knowledge*. Cambridge: Cambridge University Press.

Awater, H., Kerlin, J. R., Evans, K. K., & Tong, F. (2005). Cortical representation of space around the blind spot. *Journal of Neurophysiology, 94*(5), 3314–3324. https://doi.org/10.1152/jn.01330.2004.

Azim, E., Jiang, J., Alstermark, B., & Jessell, T. M. (2014). Skilled reaching relies on a V2a propriospinal internal copy circuit. *Nature, 508*(7496), 357–363. https://doi.org/10.1038/nature13021.

Azzi, J. C., Gattass, R., Lima, B., Soares, J. G., & Fiorani, M. (2015). Precise visuotopic organization of the blind spot representation in primate V1. *Journal of Neurophysiology, 113*(10), 3588–3599. https://doi.org/10.1152/jn.00418.2014.

Bartels, A. (2006). Defending the structural concept of representation. *Theoria, 21*(55), 7–19.

Bastian, J. (1996). Plasticity in an electrosensory system. I. General features of a dynamic sensory filter. *Journal of Neurophysiology, 76*(4), 2483–2496.

Bauer, R. H., & Fuster, J. M. (1976). Delayed-matching and delayed-response deficit from cooling dorsolateral prefrontal cortex in monkeys. *Journal of Comparative and Physiological Psychology, 90*(3), 293–302.

Baylor, D. A. (1987). Photoreceptor signals and vision. Proctor lecture. *Investigative Ophthalmology & Visual Science, 28*(1), 34–49.

Bechtel, W. (2008). *Mental mechanisms: Philosophical perspectives on cognitive neuroscience*. London: Routledge.

Bechtel, W. (2016). Investigating neural representations: The tale of place cells. *Synthese, 193*(5), 1287–1321.

Beer, R., & Williams, P. (2014). Information processing and dynamics in minimally cognitive agents. *Cognitive Science, 39,* 1–38.

Bell, C. C. (1981). An efference copy which is modified by reafferent input. *Science, 214*(4519), 450–453.

Bell, C. C. (1982). Properties of a modifiable efference copy in an electric fish. *Journal of Neurophysiology, 47*(6), 1043–1056.

Bell, C. C., Libouban, S., & Szabo, T. (1983). Pathways of the electric organ discharge command and its corollary discharges in mormyrid fish. *Journal of Comparative Neurology, 216*(3), 327–338. https://doi.org/10.1002/cne.902160309.

Bialek, W., & Rieke, F. (1992). Reliability and information transmission in spiking neurons. *Trends in Neurosciences, 15*(11), 428–434.

Bickle, J. (2003). *Philosophy and neuroscience: A Ruthlessly reductive approach*. Dordrecht: Kluwer.

Blasdel, G. G. (1992). Orientation selectivity, preference, and continuity in monkey striate cortex. *Journal of Neuroscience, 12*(8), 3139–3161.

Bolhuis, J. J., & Everaert, M. (2013). *Birdsong, speech, and language: Exploring the evolution of mind and brain*. Cambridge, MA: MIT Press.

Bolkan, S. S., Stujenske, J. M., Parnaudeau, S., Spellman, T. J., Rauffenbart, C., Abbas, A. I., et al. (2017). Thalamic projections sustain prefrontal activity during working memory maintenance. *Nature Neuroscience, 20*(7), 987–996. https://doi.org/10.1038/nn.4568.

Boone, W., & Piccinini, G. (2016). The cognitive neuroscience revolution. *Synthese, 193*(5), 1509–1534.

Born, R. T., & Bradley, D. C. (2005). Structure and function of visual area MT. *Annual Review of Neuroscience, 28,* 157–189. https://doi.org/10.1146/annurev.neuro.26.041002.131052.

Bourget, D., & Mendelovici, A. (2017). Phenomenal intentionality. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy* (Spring 2017 Edition) (forthcoming). https://plato.stanford.edu/archives/spr2017/entries/phenomenal-intentionality/.

Brainard, M. S., & Doupe, A. J. (2002). What songbirds teach us about learning. *Nature, 417*(6886), 351–358. https://doi.org/10.1038/417351a.

Brandom, R. B. (1994). *Making it explicit: Reasoning, representing, and discursive commitment*. Cambridge, MA: Harvard University Press.

Brecht, M., Schneider, M., Sakmann, B., & Margrie, T. W. (2004). Whisker movements evoked by stimulation of single pyramidal cells in rat motor cortex. *Nature, 427*(6976), 704–710. https://doi.org/10.1038/nature02266.

Briggman, K. L., Helmstaedter, M., & Denk, W. (2011). Wiring specificity in the direction-selectivity circuit of the retina. *Nature, 471*(7337), 183–188. https://doi.org/10.1038/nature09818.

Brooks, R. (1991). Intelligence without representation. *Artificial Intelligence*, *47*(1–3), 139–159.

Brooks, J. X., Carriot, J., & Cullen, K. E. (2015). Learning to expect the unexpected: Rapid updating in primate cerebellum during voluntary self-motion. *Nature Neuroscience, 18*(9), 1310–1317. https://doi.org/10.1038/nn.4077.

Buchanan, T. S., Lloyd, D. G., Manal, K., & Besier, T. F. (2004). Neuromusculoskeletal modeling: Estimation of muscle forces and joint moments and movements from measurements of neural command. *Journal of Applied Biomechanics, 20*(4), 367–395.

Bullock, T. H. (1982). Electroreception. *Annual Review of Neuroscience, 5,* 121–170. https://doi.org/10.1146/annurev.ne.05.030182.001005.

Burge, T. (2010). *Origins of objectivity*. Oxford: Oxford University Press.

Burnston, D. C. (2016a). Computational neuroscience and localized neural function. *Synthese, 193*(12), 3741–3762.

Burnston, D. C. (2016b). A contextualist approach to functional localization in the brain. *Biology and Philosophy, 31*(4), 527–550.

Butterfill, S. A., & Sinigaglia, C. (2014). Intention and motor representation in purposive action. *Philosophy and Phenomenological Research, 88*(1), 119–145.

Carlson, B. A. (2002). Neuroanatomy of the mormyrid electromotor control system. *Journal of Comparative Neurology, 454*(4), 440–455. https://doi.org/10.1002/cne.10462.

Castro, A. J. (1972). The effects of cortical ablations on digital usage in the rat. *Brain Research, 37*(2), 173–185.

Cerminara, N. L., Apps, R., & Marple-Horvat, D. E. (2009). An internal model of a moving visual target in the lateral cerebellum. *Journal of Physiology, 587*(2), 429–442. https://doi.org/10.1113/jphysiol.2008.163337.

Chang, H. (2004). *Inventing temperature: Measurement and scientific progress*. New York: Oxford University Press.

Chang, H. T., Ruch, T. C., & Ward, A. A., Jr. (1947). Topographical representation of muscles in motor cortex of monkeys. *Journal of Neurophysiology, 10*(1), 39–56.

Chang, L., & Tsao, D. Y. (2017). The code for facial identity in the primate brain. *Cell, 169*(6), 1013–1028. https://doi.org/10.1016/j.cell.2017.05.011.

Chemero, A. (2009). *Radical embodied cognitive science*. Cambridge, MA: MIT Press.

Chomsky, N. (1995). Language and nature. *Mind, 104,* 1–61.

Churchland, P. S. (1986). *Neurophilosophy: Toward a unified science of the mind-brain*. Cambridge, MA: The MIT Press.

Churchland, P. M. (1989). *A neurocomputational perspective: The nature of mind and the structure of science*. Cambridge, MA: MIT Press.

Churchland, P. M. (2012). *Plato's camera: How the physical brain captures a landscape of abstract universals*. Cambridge, MA: MIT Press.

Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Ryu, S. I., & Shenoy, K. V. (2010). Cortical preparatory activity: Representation of movement or first cog in a dynamical machine? *Neuron, 68*(3), 387–400. https://doi.org/10.1016/j.neuron.2010.09.015.

Churchland, P. S., & Sejnowski, T. J. (1992). *The computational brain*. Cambridge, MA: MIT Press.

Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience, 33,* 269–298. https://doi.org/10.1146/annurev.neuro.051508.135409.

Clark, A. (1993). *Associative engines: Connectionism, concepts, and representational change*. Cambridge, MA: MIT Press.

Clark, A. (1997). The dynamical challenge. *Cognitive Science, 21,* 461–481.

Clark, A. (2016). *Surfing uncertainty: Prediction, action, and the embodied mind*. Oxford: Oxford University Press.

Clark, A., & Toribio, J. (1994). Doing without representing? *Synthese, 101,* 401–431.

Collins, T. (2010). Extraretinal signal metrics in multiple-saccade sequences. *Journal of Vision, 10*(14), 7. https://doi.org/10.1167/10.14.7.

Colombo, M. (2014). Neural representationalism, the hard problem of content and vitiated verdicts. A reply to Hutto & Myin (2013). *Phenomenology and the Cognitive Sciences, 13*(2), 257–274.

Confais, J., Kim, G., Tomatsu, S., Takei, T., & Seki, K. (2017). Nerve-specific input modulation to spinal neurons during a motor task in the monkey. *Journal of Neuroscience, 37*(10), 2612–2626. https://doi.org/10.1523/JNEUROSCI.2561-16.2017.

Cover, T. M., & Thomas, J. A. (2006). *Elements of information theory* (2nd ed.). Hoboken, NJ: Wiley.

Craik, K. (1943). *The nature of explanation*. Cambridge: Cambridge University Press.

Crapse, T. B., & Sommer, M. A. (2008). Corollary discharge across the animal kingdom. *Nature Reviews Neuroscience, 9*(8), 587–600. https://doi.org/10.1038/nrn2457.

Craver, C. F. (2007). *Explaining the brain*. Oxford: Oxford University Press.

Cummins, R. (1983). *The nature of psychological explanation*. Cambridge, MA: MIT Press.

Cummins, R. (1989). *Meaning and mental representation*. Cambridge, MA: MIT Press.

Cummins, R. (1996). *Representations, targets, and attitudes*. Cambridge, MA: MIT Press.

Daniel, P. M., & Whitteridge, D. (1961). The representation of the visual field on the cerebral cortex in monkeys. *Journal of Physiology, 159,* 203–221.

Darling, W. G., Pizzimenti, M. A., & Morecraft, R. J. (2011). Functional recovery following motor cortex lesions in non-human primates: Experimental implications for human stroke patients. *Journal of Integrative Neuroscience, 10*(3), 353–384. https://doi.org/10.1142/S0219635211002737.

DeAngelis, G. C., & Newsome, W. T. (1999). Organization of disparity-selective neurons in macaque area MT. *Journal of Neuroscience, 19*(4), 1398–1415.

Denk, W., & Horstmann, H. (2004). Serial block-face scanning electron microscopy to reconstruct three-dimensional tissue nanostructure. *PLoS Biology, 2*(11), e329. https://doi.org/10.1371/journal.pbio.0020329.

Dennett, D. C. (1987). *The intentional stance*. Cambridge, MA: MIT Press.

Dennett, D. C. (1991). *Consciousness explained.* Boston: Little, Brown and Co.

Ding, H., Smith, R. G., Poleg-Polsky, A., Diamond, J. S., & Briggman, K. L. (2016). Species-specific wiring for direction selectivity in the mammalian retina. *Nature, 535*(7610), 105–110. https://doi.org/10.1038/nature18609.

Doupe, A. J., & Kuhl, P. K. (1999). Birdsong and human speech: Common themes and mechanisms. *Annual Review of Neuroscience, 22,* 567–631. https://doi.org/10.1146/annurev.neuro.22.1.567.

Dow, B. M., Snyder, A. Z., Vautin, R. G., & Bauer, R. (1981). Magnification factor and receptive field size in foveal striate cortex of the monkey. *Experimental Brain Research, 44*(2), 213–228.

Dowling, J. E. (2012). *The retina: An approachable part of the brain* (Rev. Ed. ed.). Cambridge, MA: Belknap Press of Harvard University Press.

Downey, A. (2017). Predictive processing and the representation wars: A victory for the eliminativist (via fictionalism). *Synthese*. https://doi.org/10.1007/s11229-017-1442-8.

Dretske, F. I. (1981). *Knowledge & the flow of information* (1st ed.). Cambridge, MA: MIT Press.

Dretske, F. I. (1988). *Explaining behavior: Reasons in a world of causes*. Cambridge, MA: MIT Press.

Egan, F. (2014). How to think about mental content. *Philosophical Studies, 170*(1), 115–135.

Eliasmith, C. (2001). Attractive and in-discrete: A critique of two putative virtues of the dynamicist theory of mind. *Minds and Machines, 11,* 417–426.

Elsayed, G. F., Lara, A. H., Kaufman, M. T., Churchland, M. M., & Cunningham, J. P. (2016). Reorganization between preparatory and movement population responses in motor cortex. *Nature Communications, 7,* 13239. https://doi.org/10.1038/ncomms13239.

Feldman, D. E. (2012). The spike-timing dependence of plasticity. *Neuron, 75*(4), 556–571. https://doi.org/10.1016/j.neuron.2012.08.001.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1*(1), 1–47.

Ferretti, G. (2016). Through the forest of motor representations. *Consciousness and Cognition, 43,* 177–196. https://doi.org/10.1016/j.concog.2016.05.013.

Fetz, E. E. (1992). Are movement parameters recognizably coded in the activity of single neurons? *Behavioral and Brain Sciences, 15,* 679–690.

Fodor, J. A. (1975). *The language of thought*. Cambridge, MA: Harvard University Press.

Fodor, J. A. (1981). *Representations: Philosophical essays on the foundations of cognitive science*. Cambridge, MA: MIT Press.

Fodor, J. A. (1987). *Psychosemantics: The problem of meaning in the philosophy of mind*. Cambridge, MA: MIT Press.

Fodor, J. A. (1990). *A theory of content and other essays*. Cambridge, MA: MIT Press.

Fodor, J. A. (2008). *LOT 2: The language of thought revisited*. Oxford: Oxford University Press.

Forssberg, H., Kinoshita, H., Eliasson, A. C., Johansson, R. S., Westling, G., & Gordon, A. M. (1992). Development of human precision grip. II. Anticipatory control of isometric forces targeted for object's weight. *Experimental Brain Research, 90*(2), 393–398.

Franklin, A. (2002). *Selectivity and discord: Two problems of experiment*. Pittsburgh: University of Pittsburgh Press.

Franklin, A. (2013). *Shifting standards: Experiments in particle physics in the twentieth century*. Pittsburgh: University of Pittsburgh Press.

Franklin, A., & Perovic, S. (2016). Experiment in physics. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy* (Winter 2016 Edition). https://plato.stanford.edu/archives/win2016/entries/physics-experiment/.

Frege, G. (1892). Über Sinn und Bedeutung. In Zeitschrift für Philosophie und philosophische Kritik (Vol. 100, pp. 25–50). Translated as 'On Sense and Reference' by M. Black in Translations from the Philosophical Writings of Gottlob Frege, P. Geach and M. Black (eds. and trans.), Oxford: Blackwell, third edition, 1980.

Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1989). Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *Journal of Neurophysiology, 61*(2), 331–349. https://doi.org/10.1152/jn.1989.61.2.331.

Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1993a). Dorsolateral prefrontal lesions and oculomotor delayed-response performance: Evidence for mnemonic "scotomas". *Journal of Neuroscience, 13*(4), 1479–1497.

Funahashi, S., Chafee, M. V., & Goldman-Rakic, P. S. (1993b). Prefrontal neuronal activity in rhesus monkeys performing a delayed anti-saccade task. *Nature, 365*(6448), 753–756. https://doi.org/10.1038/365753a0.

Fuster, J. M., & Alexander, G. E. (1970). Delayed response deficit by cryogenic depression of frontal cortex. *Brain Research, 20*(1), 85–90.

Fuster, J. M., & Alexander, G. E. (1971). Neuron activity related to short-term memory. *Science, 173*(3997), 652–654.

Galison, P. (1987). *How experiments end*. Chicago: University of Chicago Press.

Galison, P. (1997). *Image and logic*. Chicago: University of Chicago Press.

Gallistel, C. R. (1990). Representations in animal cognition: An introduction. *Cognition, 37*(1–2), 1–22.

Gallistel, C. R. (2008). Learning and representation. In J. Byrne (Ed.), *Learning and memory: A comprehensive reference* (pp. 227–242). Amsterdam: Elsevier.

Gallistel, C. R., & King, A. P. (2009). *Memory and the computational brain: Why cognitive science will transform neuroscience*. New York: Wiley.

Gandhi, N. J., & Katnani, H. A. (2011). Motor functions of the superior colliculus. *Annual Review of Neuroscience, 34,* 205–231. https://doi.org/10.1146/annurev-neuro-061010-113728.

Ganguly, K., & Carmena, J. M. (2009). Emergence of a stable cortical map for neuroprosthetic control. *PLoS Biology, 7*(7), e1000153. https://doi.org/10.1371/journal.pbio.1000153.

Gardenfors, P. (1996). Cued and detached representations in animal cognition. *Behavioral Processes, 35,* 263–273.

Gardenfors, P. (2005). The detachment of thought. In C. Erneling & D. Johnson (Eds.), *Mind as a scientific subject: Between brain and culture* (pp. 323–341). Oxford: OUP.

Garzon, F. C. (2008). Towards a general theory of antirepresentationalism. *The British Journal for the Philosophy of Science, 59*(3), 259–292.

Gazzaley, A., & Nobre, A. C. (2012). Top-down modulation: Bridging selective attention and working memory. *Trends in Cognitive Sciences, 16*(2), 129–135. https://doi.org/10.1016/j.tics.2011.11.014.

Georgopoulos, A. P., & Ashe, J. (2000). One motor cortex, two different views. *Nature Neuroscience, 3*(10), 963. https://doi.org/10.1038/79882. **(author reply 964–965)**.

Georgopoulos, A. P., Kalaska, J. F., Caminiti, R., & Massey, J. T. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *Journal of Neuroscience, 2*(11), 1527–1537.

Georgopoulos, A. P., Schwartz, A. B., & Kettner, R. E. (1986). Neuronal population coding of movement direction. *Science, 233*(4771), 1416–1419.

Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience, 14*(5), 350–363. https://doi.org/10.1038/nrn3476.

Gładziejewski, P. (2016). Predictive coding and representationalism. *Synthese, 193,* 559–582.

Gładziejewski, P., & Miłkowski, M. (2017). Structural representations: Causally relevant and different from detectors. *Biology and Philosophy, 32*(3), 337–355.

Godfrey-Smith, P. (1996). *Complexity and the function of mind in nature*. Cambridge: Cambridge University Press.

Goldberg, M. E., & Wurtz, R. H. (1972). Activity of superior colliculus in behaving monkey. I. Visual receptive fields of single neurons. *Journal of Neurophysiology, 35*(4), 542–559.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*(1), 20–25.

Graziano, M. S. (2016). Ethological action maps: A paradigm shift for the motor cortex. *Trends in Cognitive Sciences, 20*(2), 121–132. https://doi.org/10.1016/j.tics.2015.10.008.

Graziano, M. S., Taylor, C. S., Moore, T., & Cooke, D. F. (2002). The cortical control of movement revisited. *Neuron, 36*(3), 349–362.

Grice, P. (1957). Meaning. *Philosophical Review, 66,* 377–388.

Griffin, D. M., Hoffman, D. S., & Strick, P. L. (2015). Corticomotoneuronal cells are "functionally tuned". *Science, 350*(6261), 667–670. https://doi.org/10.1126/science.aaa8035.

Grush, R. (2004). The emulation theory of representation: Motor control, imagery, and perception. *Behavioral and Brain Sciences, 27*(3), 377–396. **(discussion 396–442)**.

Hacking, I. (1983). *Representing and intervening*. Cambridge: Cambridge University Press.

Hahnloser, R. H., & Kotowicz, A. (2010). Auditory representations and memory in birdsong learning. *Current Opinion in Neurobiology, 20*(3), 332–339. https://doi.org/10.1016/j.conb.2010.02.011.

Hallett, M. (2000). Transcranial magnetic stimulation and the human brain. *Nature, 406*(6792), 147–150. https://doi.org/10.1038/35018000.

Hartmann, K., Thomson, E. E., Zea, I., Yun, R., Mullen, P., Canarick, J., et al. (2016). Embedding a panoramic representation of infrared light in the adult rat somatosensory cortex through a sensory neuroprosthesis. *Journal of Neuroscience, 36*(8), 2406–2424. https://doi.org/10.1523/JNEUROSCI.3285-15.2016.

Heiligenberg, W., & Bastian, J. (1984). The electric sense of weakly electric fish. *Annual Review of Physiology, 46,* 561–583. https://doi.org/10.1146/annurev.ph.46.030184.003021.

Herculano-Houzel, S. (2010). Coordinated scaling of cortical and cerebellar numbers of neurons. *Frontiers in Neuroanatomy, 4,* 12. https://doi.org/10.3389/fnana.2010.00012.

Hewitt, A. L., Popa, L. S., Pasalar, S., Hendrix, C. M., & Ebner, T. J. (2011). Representation of limb kinematics in Purkinje cell simple spike discharge is conserved across multiple tasks. *Journal of Neurophysiology, 106*(5), 2232–2247. https://doi.org/10.1152/jn.00886.2010.

Hochberg, L. R., Bacher, D., Jarosiewicz, B., Masse, N. Y., Simeral, J. D., Vogel, J., et al. (2012). Reach and grasp by people with tetraplegia using a neurally controlled robotic arm. *Nature, 485*(7398), 372–375. https://doi.org/10.1038/nature11076.

Hodgkin, A. L., & Huxley, A. F. (1939). Action potentials recorded from inside a nerve fibre. *Nature, 144,* 710–711. https://doi.org/10.1038/144710a0.

Hohwy, J. (2013). *The predictive mind*. New York: Oxford University Press.

Holdefer, R. N., & Miller, L. E. (2002). Primary motor cortical neurons encode functional muscle synergies. *Experimental Brain Research, 146*(2), 233–243. https://doi.org/10.1007/s00221-002-1166-x.

Horgan, S., & Tienson, J. (1992). Cognitive systems as dynamical systems. *Topoi, 11,* 27–43.

Horgan, T., & Tienson, J. (1996). *Connectionism and the philosophy of psychology*. Cambridge, MA: MIT Press.

Horgan, T., & Tienson, J. (2002). The intentionality of phenomenology and the phenomenology of intentionality. In D. Chalmers (Ed.), *Philosophy of mind: Classical and contemporary readings* (pp. 520–933). Oxford: Oxford University Press.

Horsley, V. (1907). Dr. Hughlings Jackson's views of the functions of the cerebellum, as Illustrated by recent research. *The British Medical Journal*, *1*(2414), 803–808.

Horsley, V. (1909). The linacre lecture on the function of the so-called motor area of the Brain. *The British Medical Journal*, *2*(2533), 121–132.

Hotton, S., & Yoshimi, J. (2010). Extending dynamical systems theory to model embodied cognition. *Cognitive Science, 35,* 444–479.

Houk, J. C., & Wise, S. P. (1995). Distributed modular architectures linking basal ganglia, cerebellum, and cerebral cortex: Their role in planning and controlling action. *Cerebral Cortex, 5*(2), 95–110.

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology, 195*(1), 215–243.

Hubel, D. H., & Wiesel, T. N. (2005). *Brain and visual perception: The story of a 25-year collaboration*. New York, NY: Oxford University Press.

Hughlings Jackson, J. (1867). Remarks on the disorderly movements of chorea and convulsion, and on localisation. *Medical Times and Gazette*, *2*, 669–670.

Hughlings Jackson, J. (1868). Notes on the physiology and pathology of the nervous system. *Medical Times and Gazette*, *2*, 696.

Hupe, J. M., James, A. C., Payne, B. R., Lomber, S. G., Girard, P., & Bullier, J. (1998). Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature, 394*(6695), 784–787. https://doi.org/10.1038/29537.

Hutto, D. D., & Myin, E. (2013). *Radicalizing enactivism*. Cambridge, MA: MIT Press.

Hutto, D. D., & Myin, E. (2014). Neural representations not needed-no more pleas, please. *Phenomenology and the Cognitive Sciences, 13*(2), 241–256.

Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology, 17*(23), R1004–R1005. https://doi.org/10.1016/j.cub.2007.10.027.

Isaac, A. (2013). Objective similarity and mental representation. *Australasian Journal of Philosophy, 91*(4), 683–704.

Ito, M. (1970). Neurophysiological aspects of the cerebellar motor control system. *International Journal of Neurology, 7*(2), 162–176.

Johansson, R. S., & Cole, K. J. (1992). Sensory-motor coordination during grasping and manipulative actions. *Current Opinion in Neurobiology, 2*(6), 815–823.

Kakei, S., Hoffman, D. S., & Strick, P. L. (1999). Muscle and movement representations in the primary motor cortex. *Science, 285*(5436), 2136–2139.

Kalaska, J. F. (2009). From intention to action: Motor cortex and the control of reaching movements. *Advances in Experimental Medicine and Biology, 629,* 139–178. https://doi.org/10.1007/978-0-387-77064-2_8.

Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: evidence for “fast mapping”. *Science, 304*(5677), 1682–1683. https://doi.org/10.1126/science.1097859.

Kandel, E. R. (2006). *In search of memory: The emergence of a new science of mind* (1st ed.). New York: W. W. Norton & Company.

Kandel, E. R. (2013). *Principles of neural science* (5th ed.). New York: McGraw-Hill.

Keijzer, F. A. (1998). Doing without representations which specify what to do. *Philosophical Psychology, 11*(3), 269–302.

Kennedy, A., Wayne, G., Kaifosh, P., Alvina, K., Abbott, L. F., & Sawtell, N. B. (2014). A temporal basis for predicting the sensory consequences of motor commands in an electric fish. *Nature Neuroscience, 17*(3), 416–422. https://doi.org/10.1038/nn.3650.

Kiefer, A., & Hohwy, J. (2017). Content and misrepresentation in hierarchical generative models. *Synthese*. https://doi.org/10.1007/s11229-017-1435-7.

Kirsh, D. (2006). *Implicit and explicit representation encyclopedia of cognitive science* (pp. 1–4). New York: Wiley.

Kitamura, T., Ogawa, S. K., Roy, D. S., Okuyama, T., Morrissey, M. D., Smith, L. M., et al. (2017). Engrams and circuits crucial for systems consolidation of a memory. *Science, 356*(6333), 73–78. https://doi.org/10.1126/science.aam6808.

Koch, C. (2004). *The quest for consciousness: A neurobiological approach*. Denver, CO: Roberts and Co.

Komatsu, H., Kinoshita, M., & Murakami, I. (2000). Neural responses in the retinotopic representation of the blind spot in the macaque V1 to stimuli for perceptual filling-in. *Journal of Neuroscience, 20*(24), 9310–9319.

Konishi, M. (1965). The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Z Tierpsychol, 22*(7), 770–783.

Korenbrot, J. I. (2012). Speed, sensitivity, and stability of the light response in rod and cone photoreceptors: Facts and models. *Progress in Retinal and Eye Research, 31*(5), 442–466. https://doi.org/10.1016/j.preteyeres.2012.05.002.

Krahe, R., & Maler, L. (2014). Neural maps in the electrosensory system of weakly electric fish. *Current Opinion in Neurobiology, 24*(1), 13–21. https://doi.org/10.1016/j.conb.2013.08.013.

Krauzlis, R. J., Lovejoy, L. P., & Zenon, A. (2013). Superior colliculus and visual spatial attention. *Annual Review of Neuroscience, 36,* 165–182. https://doi.org/10.1146/annurev-neuro-062012-170249.

Kriegel, U. (Ed.). (2013). *Phenomenal intentionality*. Oxford: Oxford University Press.

Kustov, A. A., & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature, 384*(6604), 74–77. https://doi.org/10.1038/384074a0.

Lacquaniti, F., Borghese, N. A., & Carrozzo, M. (1992). Internal models of limb geometry in the control of hand compliance. *Journal of Neuroscience, 12*(5), 1750–1762.

Lamme, V. A., Super, H., & Spekreijse, H. (1998). Feedforward, horizontal, and feedback processing in the visual cortex. *Current Opinion in Neurobiology, 8*(4), 529–535.

Leavitt, M. L., Mendoza-Halliday, D., & Martinez-Trujillo, J. C. (2017). Sustained activity encoding working memories: Not fully distributed. *Trends in Neurosciences, 40*(6), 328–346. https://doi.org/10.1016/j.tins.2017.04.004.

Leopold, D. A. (2012). Primary visual cortex: Awareness and blindsight. *Annual Review of Neuroscience, 35,* 91–109. https://doi.org/10.1146/annurev-neuro-062111-150356.

Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature, 379*(6565), 549–553. https://doi.org/10.1038/379549a0.

Lewis, J. E., & Kristan, W. B., Jr. (1998a). A neuronal network for computing population vectors in the leech. *Nature, 391*(6662), 76–79. https://doi.org/10.1038/34172.

Lewis, J. E., & Kristan, W. B., Jr. (1998b). Representation of touch location by a population of leech sensory neurons. *Journal of Neurophysiology, 80*(5), 2584–2592.

Li, P. H., Field, G. D., Greschner, M., Ahn, D., Gunning, D. E., Mathieson, K., et al. (2014). Retinal representation of the elementary visual signal. *Neuron, 81*(1), 130–139. https://doi.org/10.1016/j.neuron.2013.10.043.

Li, C. S., Padoa-Schioppa, C., & Bizzi, E. (2001). Neuronal correlates of motor performance and motor learning in the primary motor cortex of monkeys adapting to an external force field. *Neuron, 30*(2), 593–607.

Lisberger, S. G. (2009). Internal models of eye movement in the floccular complex of the monkey cerebellum. *Neuroscience, 162*(3), 763–776. https://doi.org/10.1016/j.neuroscience.2009.03.059.

Liu, L. D., & Pack, C. C. (2017). The contribution of area MT to visual motion perception depends on training. *Neuron, 95*(2), 436–446. https://doi.org/10.1016/j.neuron.2017.06.024.

Lloyd, D. G., & Besier, T. F. (2003). An EMG-driven musculoskeletal model to estimate muscle forces and knee joint moments in vivo. *Journal of Biomechanics, 36*(6), 765–776.

Loar, B. (2003). Phenomenal intentionality as the basis of mental content. In M. Hahn & B. Ramberg (Eds.), *Reflections and replies: Essays on the philosophy of Tyler Burge* (pp. 229–258). Cambridge, MA: MIT Press.

Makino, H., Ren, C., Liu, H., Kim, A. N., Kondapaneni, N., Liu, X., et al. (2017). Transformation of cortex-wide emergent properties during motor learning. *Neuron, 94*(4), 880–890. https://doi.org/10.1016/j.neuron.2017.04.015.

Maley, C. (2017). Toward analog neural computation. *Minds and Machines*. https://doi.org/10.1007/s11023-017-9442-5.

Mandik, P. (2003). Varieties of representation in evolved and embodied neural networks. *Biology and Philosophy, 18,* 95–130.

Mangel, S. C. (1991). Analysis of the horizontal cell contribution to the receptive field surround of ganglion cells in the rabbit retina. *Journal of Physiology, 442,* 211–234.

Marler, P., & Peters, S. (1981). Sparrows learn adult song and more from memory. *Science, 213*(4509), 780–782. https://doi.org/10.1126/science.213.4509.780.

Masland, R. H. (2012). The neuronal organization of the retina. *Neuron, 76*(2), 266–280. https://doi.org/10.1016/j.neuron.2012.10.002.

Matsumoto, M., & Komatsu, H. (2005). Neural responses in the macaque v1 to bar stimuli with various lengths presented on the blind spot. *Journal of Neurophysiology, 93*(5), 2374–2387. https://doi.org/10.1152/jn.00811.2004.

Matyas, F., Sreenivasan, V., Marbach, F., Wacongne, C., Barsy, B., Mateo, C., et al. (2010). Motor control by sensory cortex. *Science, 330*(6008), 1240–1243. https://doi.org/10.1126/science.1195797.

Maunsell, J. H., & van Essen, D. C. (1983). The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *Journal of Neuroscience, 3*(12), 2563–2586.

McFarland, J. M., Bondy, A. G., Saunders, R. C., Cumming, B. G., & Butts, D. A. (2015). Saccadic modulation of stimulus processing in primary visual cortex. *Nature Communications, 6,* 8110. https://doi.org/10.1038/ncomms9110.

Milkowski, M. (2013). *Explaining the computational mind*. Cambridge, MA: MIT Press.

Miller, E. K., Erickson, C. A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *Journal of Neuroscience, 16*(16), 5154–5167.

Miller, H., Rayburn-Reeves, R., & Zentall, T. (2009). What do dogs know about hidden objects? *Behavioral Processes, 81*(3), 439–446.

Millikan, R. G. (1984). *Language, thought, and other biological categories: New foundations for realism*. Cambridge, MA: MIT Press.

Millikan, R. G. (1993). *White Queen psychology and other essays for alice*. Cambridge, MA: MIT Press.

Mishkin, M., & Manning, F. J. (1978). Non-spatial memory after selective prefrontal lesions in monkeys. *Brain Research, 143*(2), 313–323.

Mooney, R. (2009). Neural mechanisms for learned birdsong. *Learning & Memory, 16*(11), 655–669. https://doi.org/10.1101/lm.1065209.

Moran, D. W., & Schwartz, A. B. (2000). One motor cortex, two different views. *Nature Neuroscience, 3*(10), 963. https://doi.org/10.1038/79880. **(author reply 963–965)**.

Morgan, A. (2014). Representations gone mental. *Synthese, 191*(2), 213–244.

Morgan, A., & Piccinini, G. (2017). Towards a cognitive neuroscience of intentionality. *Minds and Machines*. https://doi.org/10.1007/s11023-017-9437-2

Mori, S., & Zhang, J. (2006). Principles of diffusion tensor imaging and its applications to basic neuroscience research. *Neuron, 51*(5), 527–539. https://doi.org/10.1016/j.neuron.2006.08.012.

Morris, R. G., Garrud, P., Rawlins, J. N., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. *Nature, 297*(5868), 681–683.

Moser, E. I., Kropff, E., & Moser, M. B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neuroscience, 31,* 69–89. https://doi.org/10.1146/annurev.neuro.31.061307.090723.

Movshon, J. A., & Newsome, W. T. (1996). Visual response properties of striate cortical neurons projecting to area MT in macaque monkeys. *Journal of Neuroscience, 16*(23), 7733–7741.

Muckli, L., & Petro, L. S. (2013). Network interactions: non-geniculate input to V1. *Current Opinion in Neurobiology, 23*(2), 195–201. https://doi.org/10.1016/j.conb.2013.01.020.

Murray, J. D., Jaramillo, J., & Wang, X. J. (2017). Working memory and decision-making in a frontoparietal circuit model. *Journal of Neuroscience, 37*(50), 12167–12186. https://doi.org/10.1523/JNEUROSCI.0343-17.2017.

Mylopoulos, M., & Pacherie, E. (2017). Intentions and motor representations: The interface challenge. *Review of Philosophy and Psychology, 8*(2), 317–336. https://doi.org/10.1007/s13164-016-0311-6.

Nabavi, S., Fox, R., Proulx, C. D., Lin, J. Y., Tsien, R. Y., & Malinow, R. (2014). Engineering a memory with LTD and LTP. *Nature, 511*(7509), 348–352. https://doi.org/10.1038/nature13294.

Neander, K. (2012). Teleological theories of mental content. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy* (Spring 2012 Edition). https://plato.stanford.edu/archives/spr2012/entries/content-teleological/.

Neander, K. (2017). *A mark of the mental: In defense of informational teleosemantics*. Cambridge, MA: MIT Press.

Newsome, W. T., Britten, K. H., & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature, 341*(6237), 52–54. https://doi.org/10.1038/341052a0.

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience, 8*(6), 2201–2211.

Noë, A. (2010). Vision without representation. In N. Gangopadhyay, M. Madary, & F. Spicer (Eds.), *Perception, action, and consciousness: Sensiromotor dynamics and two visual systems* (pp. 245–256). Oxford: OUP.

O'Brien, G., & Opie, J. (2004). Notes toward a structuralist theory of mental representation. In H. Clapin, P. Staines, & P. Slezac (Eds.), *Representation in mind* (pp. 1–20). Amsterdam: Elsevier.

Papineau, D. (1984). Representation and explanation. *Philosophy of Science, 51,* 550–572.

Papineau, D. (1993). *Philosophical naturalism*. Oxford: Blackwell.

Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain, 60,* 389–443. https://doi.org/10.1093/brain/60.4.389.

Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Experimental Brain Research, 47*(3), 329–342.

Pfenning, A. R., Hara, E., Whitney, O., Rivas, M. V., Wang, R., Roulhac, P. L., et al. (2014). Convergent transcriptional specializations in the brains of humans and song-learning birds. *Science, 346*(6215), 1256846. https://doi.org/10.1126/science.1256846.

Phongphanphanee, P., Mizuno, F., Lee, P. H., Yanagawa, Y., Isa, T., & Hall, W. C. (2011). A circuit model for saccadic suppression in the superior colliculus. *Journal of Neuroscience, 31*(6), 1949–1954. https://doi.org/10.1523/JNEUROSCI.2305-10.2011.

Piccinini, G. (forthcoming). Nonnatural mental representation. In K. Dolega, T. Schlicht, J. Smortchkova (Eds.), *What are mental representations?* Oxford: Oxford University Press.

Piccinini, G., & Scarantino, A. (2011). Information processing, computation, and cognition. *Journal of Biological Physics, 37*(1), 1–38.

Pickering, M. J., & Clark, A. (2014). Getting ahead: Forward models and their place in cognitive architecture. *Trends in Cognitive Sciences, 18*(9), 451–456. https://doi.org/10.1016/j.tics.2014.05.006.

Pilley, J., & Reid, A. (2011). Border collie comprehends object names as verbal referents. *Behavioral Processes, 86,* 184–195.

Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience, 3*(11), 1153–1159. https://doi.org/10.1038/80676.

Poulet, J. F., & Hedwig, B. (2003). Corollary discharge inhibition of ascending auditory neurons in the stridulating cricket. *Journal of Neuroscience, 23*(11), 4717–4725.

Poulet, J. F., & Hedwig, B. (2006). The cellular basis of a corollary discharge. *Science, 311*(5760), 518–522. https://doi.org/10.1126/science.1120847.

Prather, J. F., Peters, S., Nowicki, S., & Mooney, R. (2010). Persistent representation of juvenile experience in the adult songbird brain. *Journal of Neuroscience, 30*(31), 10586–10598. https://doi.org/10.1523/JNEUROSCI.6042-09.2010.

Pruszynski, J. A., Omrani, M., & Scott, S. H. (2014). Goal-dependent modulation of fast feedback responses in primary motor cortex. *Journal of Neuroscience, 34*(13), 4608–4617. https://doi.org/10.1523/JNEUROSCI.4520-13.2014.

Purves, D. (2018). *Neuroscience* (6th ed.). New York: Oxford University Press.

Qi, X. L., Katsuki, F., Meyer, T., Rawley, J. B., Zhou, X., Douglas, K. L., et al. (2010). Comparison of neural activity related to working memory in primate dorsolateral prefrontal and posterior parietal cortex. *Frontiers in Systems Neuroscience, 4,* 12. https://doi.org/10.3389/fnsys.2010.00012.

Quintana, J., Yajeya, J., & Fuster, J. M. (1988). Prefrontal representation of stimulus attributes during delay tasks. I. Unit activity in cross-temporal integration of sensory and sensory-motor information. *Brain Research, 474*(2), 211–221.

Raja, V. (2017). A theory of resonance: Towards an ecological cognitive architecture. *Minds and Machines*. https://doi.org/10.1007/s11023-017-9431-8.

Ramirez, S., Liu, X., Lin, P. A., Suh, J., Pignatelli, M., Redondo, R. L., et al. (2013). Creating a false memory in the hippocampus. *Science, 341*(6144), 387–391. https://doi.org/10.1126/science.1239073.

Ramsey, F. P. (1931). *The foundations of mathematics, and other logical essays*. London: Routledge and Kegan Paul.

Ramsey, W. M. (2007). *Representation reconsidered.* Cambridge: Cambridge University Press.

Ramsey, W. M. (2016). Untangling two questions about mental representation. *New Ideas in Psychology, 40,* 3–12.

Reijmers, L. G., Perkins, B. L., Matsuo, N., & Mayford, M. (2007). Localization of a stable neural correlate of associative memory. *Science, 317*(5842), 1230–1233. https://doi.org/10.1126/science.1143839.

Richmond, B. J., & Wurtz, R. H. (1980). Vision during saccadic eye movements. II. A corollary discharge to monkey superior colliculus. *Journal of Neurophysiology, 43*(4), 1156–1167.

Riley, M. R., & Constantinidis, C. (2016). Role of prefrontal persistent activity in working memory. *Frontiers in Systems Neuroscience*. https://doi.org/10.3389/fnsys.2015.00181.

Roberts, T. F., Gobes, S. M., Murugan, M., Olveczky, B. P., & Mooney, R. (2012). Motor circuits are required to encode a sensory model for imitative learning. *Nature Neuroscience, 15*(10), 1454–1459. https://doi.org/10.1038/nn.3206.

Robinson, D. L., & Wurtz, R. H. (1976). Use of an extraretinal signal by monkey superior colliculus neurons to distinguish real from self-induced stimulus movement. *Journal of Neurophysiology, 39*(4), 852–870.

Rockland, K. S., & Knutson, T. (2000). Feedback connections from area MT of the squirrel monkey to areas V1 and V2. *Journal of Comparative Neurology, 425*(3), 345–368.

Rodieck, R. W. (1998). *The first steps in seeing*. Sunderland, MA: Sinauer Associates.

Roska, B., & Werblin, F. (2001). Vertical interactions across ten parallel, stacked representations in the mammalian retina. *Nature, 410*(6828), 583–587. https://doi.org/10.1038/35069068.

Rossignol, S., & Bouyer, L. (2004). Adaptive mechanisms of spinal locomotion in cats. *Integrative and Comparative Biology, 44*(1), 71–79. https://doi.org/10.1093/icb/44.1.71.

Rouse, J. (2015). *Articulating the world: Conceptual understanding and the scientific image* (423 pp.). University of Chicago Press.

Rust, N. (2014). Population-based representations: From implicit to explicit. In M. Gazzaniga & G. Ronald (Eds.), *The cognitive neurosciences* (5th ed., pp. 337–347). Cambridge: MIT Press.

Ryder, D. (2004a). SINBAD neurosemantics: A theory of mental representation. *Mind and Language, 19*(2), 211–240.

Ryder, D. (2004b). *Models in the brain*. Oxford: Oxford University Press.

Ryle, G. (1949). *The concept of mind*. London: Hutchinson's University Library.

Salinas, E., & Abbott, L. F. (1995). Transfer of coded information from sensory to motor networks. *Journal of Neuroscience, 15*(10), 6461–6474.

Salzman, C. D., Britten, K. H., & Newsome, W. T. (1990). Cortical microstimulation influences perceptual judgements of motion direction. *Nature, 346*(6280), 174–177. https://doi.org/10.1038/346174a0.

Salzman, C. D., Murasugi, C. M., Britten, K. H., & Newsome, W. T. (1992). Microstimulation in visual area MT: Effects on direction discrimination performance. *Journal of Neuroscience, 12*(6), 2331–2355.

Sanes, J. R., & Masland, R. H. (2015). The types of retinal ganglion cells: current status and implications for neuronal classification. *Annual Review of Neuroscience, 38,* 221–246. https://doi.org/10.1146/annurev-neuro-071714-034120.

Scarantino, A. (2015). Information as a probabilistic difference maker. *Australasian Journal of Philosophy*, *93*(3), 419–443.

Scarantino, A., & Piccinini, G. (2010). Information without truth. *Metaphilosophy, 43*(3), 313–330.

Schenk, T., & Zihl, J. (1997). Visual motion perception after brain damage: I. Deficits in global motion perception. *Neuropsychologia, 35*(9), 1289–1297.

Schneider, S. (2011). *The language of thought: A new philosophical direction*. Cambridge, MA: MIT Press.

Schwartzman, R. J. (1978). A behavioral analysis of complete unilateral section of the pyramidal tract at the medullary level in Macaca mulatta. *Annals of Neurology, 4*(3), 234–244. https://doi.org/10.1002/ana.410040308.

Scott, S. H. (2000). Reply to 'one motor cortex, two different views'. *Nature Neuroscience, 3*(10), 964–965. https://doi.org/10.1038/79888.

Scott, S. H. (2016). A functional taxonomy of bottom-up sensory feedback processing for motor actions. *Trends in Neurosciences, 39*(8), 512–526. https://doi.org/10.1016/j.tins.2016.06.001.

Searle, J. (1983). *Intentionality: An essay in the philosophy of mind*. Cambridge: Cambridge University Press.

Sellars, W. (1956). Empiricism and the philosophy of mind. In H. Feigl & M. Scriven (Eds.), *Minnesota studies in the philosophy of science* (Vol. I, pp. 253–329). Minneapolis, MN: University of Minnesota Press.

Sellars, W. (1981). Mental events. *Philosophical Studies, 39,* 325–345.

Sereno, M. I. (2014). Origin of symbol-using systems: speech, but not sign, without the semantic urge. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 369*(1651), 20130303. https://doi.org/10.1098/rstb.2013.0303.

Shadmehr, R., Brandt, J., & Corkin, S. (1998). Time-dependent motor memory processes in amnesic subjects. *Journal of Neurophysiology, 80*(3), 1590–1597.

Shadmehr, R., & Krakauer, J. W. (2008). A computational neuroanatomy for motor control. *Experimental Brain Research, 185*(3), 359–381. https://doi.org/10.1007/s00221-008-1280-5.

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual Review of Neuroscience, 33,* 89–108. https://doi.org/10.1146/annurev-neuro-060909-153135.

Shagrir, O. (2012). Structural representations and the brain. *The British Journal for the Philosophy of Science, 63*(3), 519–545.

Shagrir, O. (2017). The brain as an input–output model of the world. *Minds and Machines*. https://doi.org/10.1007/s11023-017-9443-4.

Shea, N. (2007). Consumers need information: Supplementing teleosemantics with an input condition. *Philosophy and Phenomenological Research, 75,* 404–435.

Shea, N. (2014). Exploitable isomorphism and structural representation. *Proc Aristot Soc CXIV*, 77–92.

Shepard, R., & Chipman, S. (1970). Second-order isomorphism of internal representations: Shapes of states. *Cognitive Psychology, 1*(1), 1–17.

Sherrington, C. S. (1910). Flexion-reflex of the limb, crossed extension-reflex, and reflex stepping and standing. *Journal of Physiology, 40*(1–2), 28–121.

Skotko, B. G., Andrews, E., & Einstein, G. (2005). Language and the medial temporal lobe: Evidence from HM's spontaneous discourse. *Journal of Memory and Language, 53*(3), 397–415. https://doi.org/10.1016/j.jml.2005.05.003.

Soo, F. S., Schwartz, G. W., Sadeghi, K., & Berry, M. J., 2nd. (2011). Fine spatial information represented in a population of retinal ganglion cells. *Journal of Neuroscience, 31*(6), 2145–2155. https://doi.org/10.1523/JNEUROSCI.5129-10.2011.

Sparks, D. L., Lee, C., & Rohrer, W. H. (1990). Population coding of the direction, amplitude, and velocity of saccadic eye movements by neurons in the superior colliculus. *Cold Spring Harbor Symposia on Quantitative Biology, 55,* 805–811.

Spillmann, L. (2014). Receptive fields of visual neurons: The early years. *Perception, 43*(11), 1145–1176.

Sprevak, M. (2013). Fictionalism about neural representations. *The Monist, 96,* 539–560.

Squire, L. R. (2009). The legacy of patient H.M. for neuroscience. *Neuron, 61*(1), 6–9. https://doi.org/10.1016/j.neuron.2008.12.023.

Squire, L. R., Stark, C. E., & Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience, 27,* 279–306. https://doi.org/10.1146/annurev.neuro.27.070203.144130.

Squire, L., & Wixted, J. (2015). Remembering. *Daedalus, Winter, 2015,* 53–66.

Staley, K. (1999). Golden events and statistics: What's wrong with Galison's image/logic distinction. *Perspectives on Science, 7,* 196–230.

Stampe, D. (1977). Toward a causal theory of linguistic representation. In P. A. French, T. E. Uehling Jr., & H. K. Wettstein (Eds.), *Midwest studies in philosophy: Studies in the philosophy of language* (Vol. 2, pp. 81–102). Minneapolis: University of Minnesota Press.

Standing, L. (1973). Learning 10,000 pictures. *Quarterly Journal of Experimental Psychology, 25*(2), 207–222. https://doi.org/10.1080/14640747308400340.

Stangor, C. (2011). *Introduction to Psychology*. Saylor Academy.

Stich, S. (1983). *From Folk psychology to cognitive science: The case against belief*. Cambridge, MA: MIT Press.

Sullivan, J. A. (2009). The multiplicity of experimental protocols: A challenge to reductionist and non-reductionist models of the unity of neuroscience. *Synthese, 167,* 511–539.

Sullivan, J. A. (2010). A role for representation in cognitive neurobiology. *Philosophy of Science, 77*(5), 875–887.

Sussillo, D., Churchland, M. M., Kaufman, M. T., & Shenoy, K. V. (2015). A neural network that finds a naturalistic solution for the production of muscle activity. *Nature Neuroscience, 18*(7), 1025–1033. https://doi.org/10.1038/nn.4042.

Swoyer, C. (1991). Structural representation and surrogative reasoning. *Synthese, 87*(3), 449.

Takeda, K., & Funahashi, S. (2002). Prefrontal task-related activity representing visual cue location or saccade direction in spatial working memory tasks. *Journal of Neurophysiology, 87*(1), 567–588. https://doi.org/10.1152/jn.00249.2001.

Thomson, E. E., & Kristan, W. B. (2005). Quantifying stimulus discriminability: A comparison of information theory and ideal observer analysis. *Neural Computation, 17*(4), 741–778. https://doi.org/10.1162/0899766053429435.

Todorov, E. (2000a). Direct cortical control of muscle activation in voluntary arm movements: A model. *Nature Neuroscience, 3*(4), 391–398. https://doi.org/10.1038/73964.

Todorov, E. (2000b). Reply to 'one motor cortex, two different views'. *Nature Neuroscience, 3*(10), 964. https://doi.org/10.1038/79886.

Todorov, E. (2000c). Reply to 'one motor cortex, two different views'. *Nature Neuroscience, 3*(10), 963–964. https://doi.org/10.1038/79884.

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, *21*, 753–759.

Tootell, R. B., Switkes, E., Silverman, M. S., & Hamilton, S. L. (1988). Functional anatomy of macaque striate cortex. II. Retinotopic organization. *Journal of Neuroscience, 8*(5), 1531–1568.

Truccolo, W., Friehs, G. M., Donoghue, J. P., & Hochberg, L. R. (2008). Primary motor cortex tuning to intended movement kinematics in humans with tetraplegia. *Journal of Neuroscience, 28*(5), 1163–1178. https://doi.org/10.1523/JNEUROSCI.4415-07.2008.

Umilta, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., et al. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences, 105*(6), 2209–2213. https://doi.org/10.1073/pnas.0705985105.

Ungerleider, L. G., & Desimone, R. (1986). Cortical connections of visual area MT in the macaque. *Journal of Comparative Neurology, 248*(2), 190–222. https://doi.org/10.1002/cne.902480204.

van Gelder, T. (1995). What might cognition be, if not computation. *The Journal of Philosophy, 92*(7), 345–381.

Varela, F. J., Thompson, E., & Rosch, E. (2017). *The embodied mind* (Revised ed.). Cambridge, MA: MIT Press.

Volkinshtein, D., & Meir, R. (2011). Delayed feedback control requires an internal forward model. *Biological Cybernetics, 105*(1), 41–53. https://doi.org/10.1007/s00422-011-0450-x.

Wandell, B. A. (1995). *Foundations of vision*. Sunderland, MA: Sinauer Associates.

Waskan, J. (2006). *Models and cognition: Prediction and explanation in everyday life and in science*. Cambridge, MA: The MIT Press.

Watanabe, Y., & Funahashi, S. (2004). Neuronal activity throughout the primate mediodorsal nucleus of the thalamus during oculomotor delayed-responses. I. Cue-, delay-, and response-period activity. *Journal of Neurophysiology, 92*(3), 1738–1755. https://doi.org/10.1152/jn.00994.2003.

Weber, M. (2005). *Philosophy of experimental biology*. Cambridge: Cambridge University Press.

Weber, M. (2014). Experiment in biology. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy* (Winter 2014 Edition). https://plato.stanford.edu/archives/win2014/entries/biology-experiment/.

Wessberg, J., Stambaugh, C. R., Kralik, J. D., Beck, P. D., Laubach, M., Chapin, J. K., et al. (2000). Real-time prediction of hand trajectory by ensembles of cortical neurons in primates. *Nature, 408*(6810), 361–365. https://doi.org/10.1038/35042582.

White, B. J., Berg, D. J., Kan, J. Y., Marino, R. A., Itti, L., & Munoz, D. P. (2017). Superior colliculus neurons encode a visual saliency map during free viewing of natural dynamic video. *Nature Communications, 8,* 14263. https://doi.org/10.1038/ncomms14263.

Whitlock, J. R., Heynen, A. J., Shuler, M. G., & Bear, M. F. (2006). Learning induces long-term potentiation in the hippocampus. *Science, 313*(5790), 1093–1097. https://doi.org/10.1126/science.1128134.

Wickersham, I. R., Lyon, D. C., Barnard, R. J., Mori, T., Finke, S., Conzelmann, K. K., et al. (2007). Monosynaptic restriction of transsynaptic tracing from single, genetically targeted neurons. *Neuron, 53*(5), 639–647. https://doi.org/10.1016/j.neuron.2007.01.033.

Williams, D. (2017). Predictive processing and the representation wars. *Minds and Machines*. https://doi.org/10.1007/s11023-017-9441-6.

Wimmer, K., Nykamp, D. Q., Constantinidis, C., & Compte, A. (2014). Bump attractor dynamics in prefrontal cortex explains behavioral precision in spatial working memory. *Nature Neuroscience, 17*(3), 431–439. https://doi.org/10.1038/nn.3645.

Wolpert, D. M., & Miall, R. C. (1996). Forward models for physiological motor control. *Neural Networks, 9*(8), 1265–1279.

Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences, 2*(9), 338–347.

Xu, H., Han, C., Chen, M., Li, P., Zhu, S., Fang, Y., et al. (2016). Rivalry-like neural activity in primary visual cortex in anesthetized monkeys. *Journal of Neuroscience, 36*(11), 3231–3242. https://doi.org/10.1523/JNEUROSCI.3660-15.2016.

Yizhar, O., Fenno, L. E., Davidson, T. J., Mogri, M., & Deisseroth, K. (2011). Optogenetics in neural systems. *Neuron, 71*(1), 9–34. https://doi.org/10.1016/j.neuron.2011.06.004.

Zylberberg, J., & Strowbridge, B. W. (2017). Mechanisms of persistent activity in cortical circuits: Possible neural substrates for working memory. *Annual Review of Neuroscience, 40,* 603–627. https://doi.org/10.1146/annurev-neuro-070815-014006.