

# Closing Dewey's Circuit

A. Wallach\*, S. Marom<sup>†</sup> and E. Ahissar<sup>‡</sup>

\*University of Ottawa, Ottawa, ON, Canada, <sup>†</sup>Technion—Israel Institute of Technology, Haifa, Israel, <sup>‡</sup>The Weizmann Institute of Science, Rehovot, Israel

## 1 INTRODUCTION

One hundred and twenty years ago, the American philosopher and psychologist John Dewey (Fig. 1) published his seminal paper *The Reflex Arc Concept in Psychology* in the *Psychological Review* (Dewey, 1896). In this paper, Dewey challenged the reflex arc, a by-then (and since then, as we will soon demonstrate) consensual unifying framework for action and perception. The framework, advanced by European experimental psychologists, pertains to a general interpretation that was referred to, at the time, as “structural psychology.” Advocates of this framework, which Dewey so fiercely opposed, viewed psychological processes as sequences of distinct steps that are executed in a timely and precise manner. The structure of the system—the identity and location of the elements executing the different stages of the process—is at the epicenter of interest. Dewey, a key proponent of the philosophy of Pragmatism and one of the founders of the Chicago group of psychologists, sought to advance an alternative, “functional psychology,” focussing on system-environment interactions and their value in achieving functionally meaningful goals. Functional psychologists did not ignore or deny the impacts of structures and mechanisms inherent to the individual in the emergence of behavior; likewise, structural psychologists did not ignore or deny the functional attributes of behavior. Rather, the main difference between these two strands of academic psychology pertained to the methods that are most likely to produce understanding of behavior. Structuralists sought to identify program-like processes hidden deep inside the machine, the human brain; functionalists could not see how the emergence of behavior can be understood in isolation from coupled subject-environment dynamics. In this context, Marom (2015) offered to use the more indicative terms *structural-programmatic* and *functional-dynamic* to designate the two stances.<sup>1</sup>

1. For a concise review of the structural versus functional split in behavioral and brain sciences at the turn of the 20th century, see Marom (2015, pp. 138–148).

In this chapter, we juxtapose these two stances, discuss the methodological reasons for the dominance of the structural-programmatic stance in neuroscience, and offer closed-loop methodologies as a functional-dynamic alternative for studying action and perception as a complete circuit.

## 2 THE BABY AND CANDLE SCENARIO

Let us follow Dewey's footsteps by first illustrating the structural-programmatic framework with the “baby and candle” example, originally appearing in William James's *Principles of Psychology* (James, 1890). The example describes how an infant interacts with a novel object (see Fig. 2), and aims to demonstrate the mechanisms underlying existing behaviors and their modification. The scenario begins with the light of a candle stimulating the child's retina. This leads to an internal “idea” of light, which leads to a reflexive motor response of hand reaching toward the candle. A secondary chain of events then commences with the flame's heat stimulating the skin of the child's fingers, leading to an “idea” of pain, which prompts a reflexive motor response of hand retraction. Association by Succession, a well-accepted and studied principle underlying learning, ties the internal ideas of candlelight and pain to inhibit future hand reaching, and so behavior is modified.

The above analysis thus describes two *reflex arcs*, each starting with a peripheral sensory event-designated *stimulus* (flame image, fingertip burning), followed by the generation of an internal *idea* (neural representation of the stimulus) and ends with a motor action-designated *response* (hand reaching or retracting). When the scenario is described in these terms, the reflex arc seems to be the simplest model that can account for the observed behavior and thus the preferred scientific model.

However, several seemingly unrelated questions may come to the reader's mind: what caused the candlelight to appear in the baby's fovea? What was the baby seeing and feeling during either hand motion? And of course,

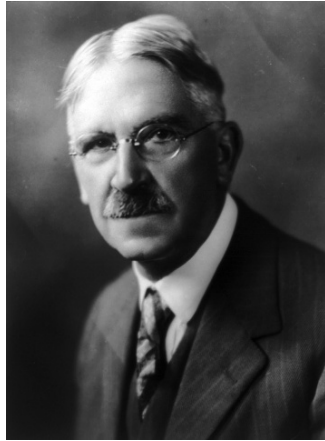


FIG. 1 John Dewey.

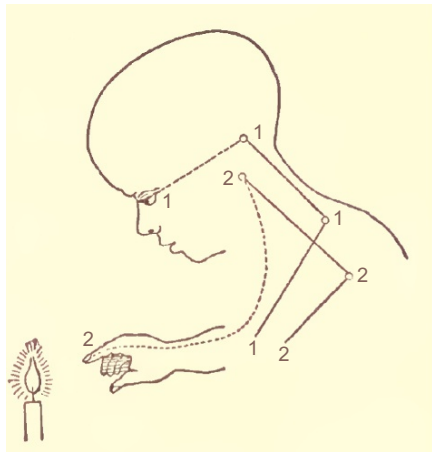


FIG. 2 Baby and candle. Two reflex arcs are depicted: seeing a candle, which leads to hand reaching (labeled 1) and feeling the candle heat, which leads to hand retraction (labeled 2). (From James, W., 1890. *The Principles of Psychology*. Holt, Reinhart and Winston, New York.)

where were the baby's parents, who so irresponsibly left an unattended baby within reach of an open flame? The picture we are left with is of a baby in solitary confinement, staring blankly and motionlessly into the void. The candle appears suddenly and unexpectedly "out of the blue" in his or her field of view. The motor responses are uncontrolled spasmodic jolts. Such overly reduced scenarios had profound impacts on the experimental research of brain and behavior.

Dewey identified the definitions of stimulus and response—the beginning and end of the arc—as the foundation stones upon which the reflex arc is built. The perceptual process is set into motion with a purely sensory event. Thought is an intermediate step and involves neither sensation nor action. And finally, the process comes to its fulfillment with a purely motor event. Each of these components—sensation, thought, and action—is regarded as being distinct in both its timing and nature, running in

turns like workstations in an efficient assembly line or sub-routines in a computer program. The breaking up of the arc into these separate, disjoint processes is an inescapable consequence of viewing sensation as the initiation (stimulus) and action as the conclusion (response) of the perceptual process.

### 3 THE CIRCUIT ALTERNATIVE

The arc concept fails to acknowledge the circular nature of natural perception. "What we have is a circuit, not an arc or broken segment of a circle" says Dewey, referring to the fact that actions are precursors, in fact prerequisites to sensation. Dewey termed the complete circuit *coordination*—a dynamic sensory-motor process that underlies perception. Each of the stages in the baby and candle example (seeing the candle, forming an idea of the candle, reaching the hand toward it, etc.) involves in fact both sensation and action, working at the same time and having equal importance in the emergence of perception. This necessary connection between action and sensation was demonstrated in countless elegant experiments since Dewey published his paper (Ahissar and Arieli, 2001; Held and Hein, 1963; Kleinfeld et al., 2006; König and Luksch, 1998; Land, 2006; Lederman and Klatzky, 1987; Prescott et al., 2011; Rucci et al., 2007; Schroeder et al., 2010; Yarbus, 1967).

When all stages of an interaction are acknowledged to be both motor and sensory, the choice of a start- and end-point to the perceptual process becomes completely arbitrary; instead, what we have is a continuous sequence of motor-sensory coordinations, all linked to one another (a "circle," in Dewey's terminology); the oculomotor coordination of seeing the candle is preceded by a different coordination, for instance, by smelling smoke (an olfactory-sniffing coordination), and followed by scanning the candle and hand reaching. These motor-sensory coordinations are in fact constituents of a larger-scale coordination, that of interacting with an object. This coordination is, in turn, part of an even larger one, for instance that of exploring a new room, and so on in a nested, hierarchical manner.<sup>2</sup> Thus the association of a flame with pain is a natural outcome of the image and the pain pertaining to the same coordination, rather than necessitating an additional, external process that mediates between two distinct reflex arcs. Each large-scale coordination also provides context to its constituents, a context which is essential for their interpretation. For instance, the smell of smoke carries a different meaning and entails a different response if one is lighting a candle, baking a cake, or driving a car.

The circuit view removes the need for any cause (either internal or external) for setting the perceptual process in motion; it is always in motion, "one uninterrupted, continuous redistribution of mass," with the different events

2. Another type of coordination not addressed by Dewey, that of interactions between subjects, is discussed later in this chapter.

and interactions only reshaping and redirecting it. In other words, rather than viewing perception as a program or an algorithm, it is viewed as a physical dynamical process, similar to the ever-changing wind currents in the atmosphere; winds are entailed by air-pressure gradients, which they in turn equilibrate. Yet neither the wind nor the pressure is regarded as “stimulus” or “response.”

#### 4 DYNAMICS OF PERCEPTION

A school of researchers have advanced the characterization of perception as a dynamical process (Ahissar and Vaadia, 1990; Ashby, 1952; Kelso, 1997; O'Regan and Noe, 2001; Port and Van Gelder, 1995; Powers, 1973; Wiener, 1949). First, like all dynamical processes, perception takes time. The first wave of sensory-driven neuronal activity typically reaches most of the relevant cortical areas within ~100 ms, and with vision quick saccadic reports on the crude category of the perceived item can be generated as fast as 150 ms (Wu et al., 2014). Yet, identification of more delicate categories, or perception of item details, takes typically hundreds of ms from first sensor-object encounter, a period during which perceptual acuity continuously improves (Micheyl et al., 2012; Packer and Williams, 1992; Saig et al., 2012).

Studies performed in rodent and human tactile perception revealed that this gradual improvement in acuity coincides with a behavioral and neuronal process of convergence. For instance, object features, such as location and texture, are perceived via a sequence of several sensor-object interactions whose motor aspects show a pattern of convergence toward asymptotic values (Chen et al., 2015; Horev et al., 2011; Knutsen et al., 2006; McDermott et al., 2013; Saig et al., 2012; Saraf-Sinik et al., 2015). Convergence processes, ie, dynamic processes during which the state of the system gradually approaches a steady state, are hallmarks of closed-loops. When the different components of the system—sensation, motor, and neuronal—all converge together, they are likely to play part in the same closed-loop.

As noted earlier, the closed-circuit view of perception grants equal importance to motor and sensory dynamics (Ahissar and Vaadia, 1990; Diamond et al., 2008; Friston, 2010; Gibson, 1962; Jarvilehto, 1999; O'Regan and Noe, 2001). Sensory signals may often be ambiguous if processed without the motor signals that yielded them. This has been explicitly demonstrated so far only for tactile perception (Gamzu and Ahissar, 2001; Horev et al., 2011; Saig et al., 2012; Saraf-Sinik et al., 2015), but should hold for any scanning sensory modality, as the nature and details of sensory signals depend on both the sampling movement (its direction, speed, and amplitude) and the sampled object (Ahissar and Arieli, 2012; Ahissar and Zacksenhouse, 2001; Bagdasarian et al., 2013). An example is the

curvature signal generated at the base of a whisker upon its contact with an object. The same curvature can be generated when contacting objects at different locations, an ambiguity that is resolved if the angle by which the whisker is rotated is taken into account (Bagdasarian et al., 2013).<sup>3</sup> Such interdependencies can be termed motor-sensory contingencies; O'Regan and Noe (2001) described how these contingencies may serve as the basis for perception and showed that they eliminate the need for an explicit internal representation of external objects.

Perception of the external environment was thus described as a process in which the brain temporarily “grasps” external objects and incorporates them in its motor-sensory loops (Ahissar and Assa, 2016; Assa and Ahissar, 2015). Such a process starts with a perturbation, internal or external, and gradually converges toward a complete inclusion, though in practice, never reaches that state. A laboratory-induced flashed stimulus, whose predominance in neuroscientific research will be discussed shortly, probes only the initiation of the perceptual process.

#### 5 THE PULL OF THE STRUCTURAL-PROGRAMMATIC VIEW

Reflecting on the study of brain and behavior in the 120 years since the publication of Dewey's paper, and particularly over recent decades, it becomes apparent that the structural-programmatic paradigm reigns supreme; it is, by and large, the guiding framework to which almost all neuroscientific endeavors adhere to, including those commanded by proponents of the functional-dynamic alternative, such as the authors of the current chapter. One can easily categorize the studies reported in the literature, especially (but not exclusively) those performed *in vivo*, into one of the three arc components: sensation (where we find themes such as neural encoding and sensory adaptation) (Szwed et al., 2003; Wallach et al., 2016), thought (internal representation, working memory, decision making) (Shahaf et al., 2008), and action (neural pattern generation and biological motor control) (Simony et al., 2010). What, thus, pulls us so irresistibly toward the structural-programmatic view, notwithstanding the overwhelming evidence for the active dynamic nature of perception?

The structural-programmatic approach is a form of reductionism, the idea that complex “macroscopic” systems and processes can (and should) be explained as the net outcome of their (supposedly) simpler “microscopic” components. In this regard, the disintegration of the reflex arc into a disjoint succession of sensation, thought, and action

3. This challenge cannot be alleviated by adding efference copy information to open-loop perceptual processing—efference copies are not accurate enough to account for perceptual accuracy (Ahissar and Assa, 2016; Simony et al., 2010).

is to the reductionist not so much an inescapable evil, but rather a desired good. This reductionist approach places the structural-programmatic view within the Newtonian tradition of the natural sciences, which also involves the isolation of systems from their environment so that they may be studied as *closed systems*. When a system cannot be hermetically “closed,” or when its behavior when closed becomes trivial, environmental variables must be added and these are typically represented by generic entities such as field, boundary conditions, or, in our case, stimulus. The underlying assumption in this procedure is that the studied system possesses some intrinsic, context-independent mechanisms that may be uncovered in isolation of its natural environment. Thus, the structural-programmatic view provides an easy-to-follow methodology, with centuries of demonstrated success in the fields of Physics and Chemistry. Before we describe this methodology in detail, we note that the applicability of reductionist approaches to living systems is hindered by two important factors: the overwhelming complexity of the systems’ components (Marom, 2015) and the ubiquity of top-down modulating processes, from the macroscopic system to its components (Noble, 2008).

To demonstrate the prevailing methodology, let’s consider a prototypic experiment in neuroscience: the perceptual task developed by Vernon B. Mountcastle and broadly utilized by many others (Britten et al., 1992; Fassihi et al., 2014; Mountcastle et al., 1975; Romo and Salinas, 2003) (Fig. 3). The experiment begins with an animal (originally a monkey) being placed in a designated chamber, well isolated from any distracting interactions with fellow subjects or with the experimenter. The relevant sensor (eg, eyes or fingers) is positioned motionlessly (either by physical restraint or by diligent training) so that it awaits stimulation (Fig. 3A, eg, fixating the eyes on a blank screen or pressing the finger against an idle vibrator). A sensory stimulus (eg, displayed image or tactile vibration) is flashed, ie, briefly presented and then removed, while the animal stays patiently idle (Fig. 3B); sometimes, the stimulation is designed to be so brief that any concomitant motor action (eg, saccades) is precluded. After an additional “waiting” epoch elapses—time for the animal to form ideas and make decisions (Fig. 3C)—a “go” signal is given and the animal provides perceptual report by executing a brief stereotypic motor action (Fig. 3D, eg, pressing a button, moving the eyes left or right). Correlations between

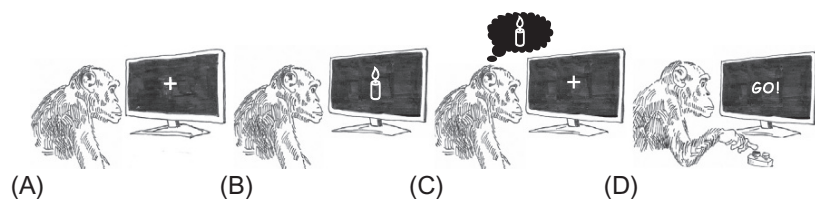
concurrently recorded neural activity and the behavioral signals are used to identify neuronal populations as being related to “stimulus encoding” (sensation), “working memory” and “decision making” (thought), “motor planning and execution” (action), or mixtures thereof.

It should become obvious by now that this experimental setup is designed with the primary objective of reenacting the “baby and candle” scenario in full within the laboratory walls. Sophisticated software and hardware and arduous training are dedicated to cast the animal’s behavior into the structural-programmatic mold, to ensure that sensation leads to thought leads to action, with minimal confluence between these components. Action is prevented from affecting sensation by prohibiting the subject from actively exploring the presented object. Furthermore, individual trials are usually designed to be mutually independent, and therefore the perceived object is, in itself, “nonrelational”—it is indifferent to the actions of the subject (an important point to which we will come back toward the end of this section).

Immobilization of the subject, essential for the experimental realization of the reflex arc, is also technically advantageous. Unlike motor responses of free-to-act subjects, sensory objects are easy to manipulate. This controllability of the experimental conditions entails reduction in the variance of the sensory input, which should (so the structural-programmatic view predicts) lead to reduction in the variance of internal processes, motor responses, and perception; such reduction of variance is always sought after, as it entails stronger, statistically significant findings. Moreover, immobilization greatly simplifies measurements of physiological and behavioral processes (eg, neuronal recordings, eye or whisker tracking, etc.); indeed, some measurements are extremely difficult to perform when the animal is awake, let alone moving about. The “reflex-arc” methodology described earlier may be implemented, to a certain degree, even in anesthetized animals, a preparation that offers unparalleled accessibility and controllability. However, since an anesthetized animal does not perceive, think, make decisions, or respond, studies in anesthetized animals focus on systematically analyzing either the ascending (sensory to thought) (Hubel and Wiesel, 1962) or descending (thought to motor) (Brecht et al., 2004) pathways of perception.

Of all the objects in an animal’s environment, the most critical for its survival are other subjects—be they parents,

**FIG. 3** Popular perceptual task. (A) Sensory organ is positioned motionlessly and awaits stimulation. (B) Sensory object is presented to the subject. (C) Object is removed; subject continues fixating while internally processing the stimulus. (D) Subject responds with a motor action.



potential mates, prey items, or predators. These are also the most challenging to perceive, as their relations with the subject, and not just their attributes, need to be discerned. Such intersubject relations are, by definition, of closed-loop nature; it is of no wonder therefore that parents are absent from the “baby and candle” reflex-arc scenario. Consequently, the reflex-arc experimental method described earlier tends almost exclusively to focus on inanimate, non-relational sensory objects. This preference stems, in part, from the wish to minimize trial-to-trial variance as much as possible. But it also originates from the reductionist assumption that “complex” objects are just the sum of their “simple” components, as discussed earlier. Thus, to the structuralists, the face of the subject’s mother is a collection of lines and surfaces; first, they think, we uncover how lines and surfaces are perceived, and later we can see how these are combined into a face “downstream” (Marr, 1982; Tanaka et al., 2014). The functional-dynamic view, however, claims that perception of mother has nothing to do with lines and surfaces. It is yet another type of high-level coordination: the on-going, closed-loop coordination between the two subjects, the child and the mother. This *relational* process, deeply rooted in phylogenetic and ontogenetic histories, brings about a functional, adaptive perception of the situation (Marom, 2015). Indeed, recent evidence suggests that relational and nonrelational objects lead to distinct neural dynamics, even in brain regions taken to be strictly sensory (Bobrov et al., 2014). In order to allow the assessment of the relevance of such processes to perception, methodologies that aim at studying perception should better allow for the inclusion of meaningful, dynamical, and responsive objects.

In this section, we described the prevailing reflex-arc like experimental setup. One cannot deny that this open-loop methodology yielded exciting results and advanced our understanding of possible workings of components of the brain. In rare cases, a complete sensory motor circuit was analyzed this way to provide a satisfactory explanation of ethologically relevant behaviors (Heiligenberg, 1991). However, given the points we raised earlier, such rare cases cannot justify the application of the structural-programmatic approach in more complex cases. Importantly, the extent of reduction imposed upon the studied system by the design of the experimental setup, choice of controlling and measured variables (Rosen, 1991), and constraints on the temporal scale of the experiment (Marom, 2010) are often overlooked. Once the open-loop constraints have been imposed on the animal and it is compelled to reenact the reflex arc, it is no wonder we see no evidence for closed-loop perceptual processes. The fact that animals can perform limited perceptual tasks within these open-loop constraints perhaps reveals the lower bounds for perception, and how far they may be extended via training, but certainly not the processes dominating natural perception.

## 6 REDEFINING STIMULUS AND RESPONSE

We have seen that the foundations of the reflex arc are the definitions of stimulus and response. Dewey suggests replacing these definitions with ones befitting the functional-dynamic view. Instead of a purely sensory event, the stimulus is “something to be discovered; to be made out,” namely a state in the motor-sensory coordination space in which a “conflict [arises] within the coordination.” In the language of dynamical systems, we would call such a state a *separatrix*—a region in state-space from which the dynamics may progress toward one of several basins of attraction. Likewise, the response is not a motor action, but “whatever will serve to complete the disintegrating coordination”; it is the dynamics in the coordination which settle the above-mentioned conflict. In other words, it is the aforementioned convergence of the motor-sensory dynamics into a stable attractor (Ahissar and Assa, 2016; Assa and Ahissar, 2015). Such convergence need not be complete (in fact it never is, as this would require infinite time); it suffices that stability of the coordination is reconstituted (Horev et al., 2011; Saig et al., 2012). Because of the nested, hierarchical organization of different levels of closed-loop perceptual processes, once a low-level coordination converges sufficiently, the high-level one in which it is embedded may stimulate it once more, throwing it into a new separatrix (eg, executing a saccade to another, yet-to-be-perceived object). With these new definitions we can now offer alternative methodologies to advance the functional, close-circuit approach.

## 7 USING CLOSED-LOOP METHODOLOGY

As we have demonstrated, the root cause for the dominance of the structural-programmatic view in neuroscience is the open-loop methodology which reenacts the reflex arc. Proponents of the functional-dynamic view fell short of providing a satisfactory alternative methodology. It is perhaps ironic that the functional-dynamic view, which pertains to the Pragmatic philosophy, failed at the acid-test for ideas in that philosophy: “... to develop a thought’s meaning, we need only determine what conduct it is fitted to produce.”<sup>4</sup> What is the experimental conduct that is derived from the functional-dynamic view? What simple and applicable methodology allows for the study of action and perception in a holistic manner?

One option is to experiment with animals that are free to move and act. This approach is gaining popularity as the technology needed for such experiments is rapidly advancing: miniaturization allows recordings of neural

---

4. James, citing Pierce, in Pragmatism, Lecture II.

activity from freely walking (O’Keefe and Dostrovsky, 1971), swimming (Canfield and Mizumori, 2004), or even flying (Yartsev and Ulanovsky, 2013) subjects, while advanced video processing and data analysis enable high-resolution tracking of free behavior (Jun et al., 2014; Knutsen et al., 2005). Such experiments yielded important findings, particularly in the study of memory and navigation, and appear to be highly promising for studying unconstrained perception. Some studies demonstrated how neuronal activity changes in the freely moving versus immobilized contexts (Oram et al., 2015). This approach faces two major challenges. First, it is highly demanding in terms of recording techniques and experimental design. Secondly, it requires forsaking much of the control over the perceptual process, as the subject chooses how to interact with the environment; each subject will do so differently, and even the same subject will never repeat the same trajectory twice. This lack of control is further aggravated if one wishes to study relational dynamics between subjects, as this involves several (at least two) acting agents.

The alternative we wish to advance here is of using closed-loop methodology as a way to perform systematic studies of perception while allowing natural interactions between the subject and the environment. Like the classic perceptual task described earlier, the sensory input in the relevant modality is controlled by the experimental setup; this may involve partial or complete immobilization and even anesthesia. The difference, however, is that this sensory flow is not predetermined and fixed, but responds on-line to the actions of the subject that are detected in real-time. What the experimenter controls and manipulates is the set of rules governing these environmental responses. In other words, the closed-loop experimental setup completes the reflex arc into a circuit; how the circuit is closed (ie, what sensations are generated in response to any detected action) defines the nature of the controlled environment in which the subject is situated.

Several recent studies followed this direction of using closed-loop methodology to create a well-controlled responsive environment. An emerging technique is to construct a “virtual reality” environment to provide the illusion of free exploration in immobilized animals (Dombeck et al., 2010; Tammero and Dickinson, 2002). The strongest drive for the development of such setups is technical, as it allows using advanced techniques (eg, calcium imaging or fMRI) to study subject-environment interactions. Most of these studies, while providing fascinating new results, still base their analyses on the structural-programmatic stimulus-response definitions described earlier.

A number of studies went the extra mile of using closed-loop methodology to study how different environmental contexts affect neural and behavioral dynamics. Ahrens et al. (2012) manipulated the rules of environmental feedback to study the convergence processes that govern

closed-loop locomotion in zebra fish larva. Keller et al. (2012) recorded neuronal activity in the primary visual cortex, a region that (according to the structural-programmatic view) is regarded as an early stage in the “algorithm” that extracts basic features (eg, line orientation and color) from the visual scene (Marr, 1982). By comparing the neuronal activity under closed-loop virtual reality settings and when the loop is opened, Keller and colleagues demonstrated that this region integrates both sensory and motor information. Marom and Wallach (2011) asked human subjects to report on the perception of ambiguous objects displayed in a very similar method to Mountcastle’s perceptual task described earlier. The circuit was closed by allowing the level of ambiguity to respond to the subject’s perceptual reports, and the dynamics under this closed-loop relational context were compared with those in the static “reflex-arc” case. Contrary to the prediction of the structural-programmatic view, the added trial-to-trial variability of the sensory input in the closed-loop setting reduced (rather than enhanced) the variance in perception, indicating that perceptual variability is not simply reflecting internal “noise.” Rather, it suggests an innate exploration for relational dynamics with the perceived object.

Closed-loop methodology can be used to study the functioning of individual components within a circuit. For example, as sensory pathways evolved to operate in conjunction with the motor pathways that actuate their sensory organs, studying these pathways in open-loop conditions might miss their major functional characteristics. In animal models, one can close the loop between a given sensory station and its relevant sensory organ via artificial actuators and motor control algorithms. Such hybrid systems (Wallach et al., 2016) allow both the study of the sensory pathway in a closed-loop condition, and the investigation of the plausibility of candidate motor control algorithms.

Closed-loop methodology also enables the introduction of relational objects that mimic the behavior of ethologically significant subjects. The rules of feedback can be altered to give rise to different intersubject dynamics. For instance, in the case of conspecific rivalry, one can study what aspects of these relational dynamics determine whether a subject converges into a dominant or a subordinate role.

Finally, analysis of perceptual dynamics could be aided by complementing the closed-loop methodology with the functional-dynamic definitions of stimulus and response discussed in the previous section. This involves confronting the subject with perceptual ambiguities (stimuli) and analyzing the processes of convergence (responses) both in behavior (of the subject and of the responsive environment) and in physiology. The closed-loop setup can be used to investigate, in the laboratory, the dynamics around naturally occurring states. For example, subjects can be actively directed toward the aforementioned “separatrices” and

maintained there; in the above-mentioned study by Marom and Wallach, for instance, the feedback was used to keep the object just at the threshold of detection. Similar approaches can be used to keep bi-stable objects with dual-meanings (eg, Necker cubes) just at the borderline between two basins of attractions. Adhering to Dewey's alternative definitions of stimulus and response may thus help us anchor our attention to the functional-dynamic interpretations, an antidote or counterbalance to the ever-present temptation of structural-programmatic simplicity.

## 8 CONCLUSIONS

In this chapter we aim to show how the closed-circuit, functional-dynamic framework so eloquently described by Dewey, failed to supersede the reflex arc view of perception, despite the persuasive evidence accumulated over the past 120 years. This dominance of the structural-programmatic framework is largely owing to the simple experimental and analytical reduction that supports it, illustrated here by the baby and candle scenario and its laboratorial reenactments. Closed-loop methodology, complemented by Dewey's functional-dynamic definitions of stimulus and response, is offered as a way to complete the arc into a full circuit.

## REFERENCES

- Ahissar, E., Arieli, A., 2001. Figuring space by time. *Neuron* 32, 185–201.
- Ahissar, E., Arieli, A., 2012. Seeing via miniature eye movements: a dynamic hypothesis for vision. *Front. Comput. Neurosci.* 6, 89.
- Ahissar, E., Assa, E., 2016. Perception as a closed-loop convergence process. *eLife* 12830.
- Ahissar, E., Vaadia, E., 1990. Oscillatory activity of single units in a somatosensory cortex of an awake monkey and their possible role in texture analysis. *Proc. Natl. Acad. Sci. U. S. A.* 87, 8935–8939.
- Ahissar, E., Zacksenhouse, M., 2001. Temporal and spatial coding in the rat vibrissal system. *Prog. Brain Res.* 130, 75–88.
- Ahrens, M.B., Li, J.M., Orger, M.B., Robson, D.N., Schier, A.F., Engert, F., et al., 2012. Brain-wide neuronal dynamics during motor adaptation in zebrafish. *Nature* 485 (7399), 471–477.
- Ashby, W.R., 1952. *Design for a Brain*. Chapman & Hall, London.
- Assa, E., Ahissar, E., 2015. Motor-sensory closed-loop perception (CLP) models and robotic implementation. In: Paper Presented at the IROS 2015 Workshop on Sensorimotor Contingencies for Robotics.
- Bagdasarian, K., Szwed, M., Knutsen, P.M., Deutsch, D., Derdikman, D., Pietr, M., et al., 2013. Pre-neuronal morphological processing of object location by individual whiskers. *Nat. Neurosci.* 16 (5), 622–631.
- Bobrov, E., Wolfe, J., Rao, R.P., Brecht, M., 2014. The representation of social facial touch in rat barrel cortex. *Curr. Biol.* 24 (1), 109–115.
- 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, 704–710.
- Britten, K.H., Shadlen, M.N., Newsome, W.T., Movshon, J.A., 1992. The analysis of visual motion: a comparison of neuronal and psychophysical performance. *J. Neurosci.* 12 (12), 4745–4765.
- Canfield, J.G., Mizumori, S.J., 2004. Methods for chronic neural recording in the telencephalon of freely behaving fish. *J. Neurosci. Methods* 133 (1), 127–134.
- Chen, J.L., Margolis, D.J., Stankov, A., Sumanovski, L.T., Schneider, B.L., Helmchen, F., 2015. Pathway-specific reorganization of projection neurons in somatosensory cortex during learning. *Nat. Neurosci.* 18, 1101–1108.
- Dewey, J., 1896. The reflex arc concept in psychology. *Psychol. Rev.* 3 (4), 357.
- Diamond, M.E., von Heimendahl, M., Knutsen, P.M., Kleinfeld, D., Ahissar, E., 2008. 'Where' and 'what' in the whisker sensorimotor system. *Nat. Rev. Neurosci.* 9 (8), 601–612.
- Dombeck, D.A., Harvey, C.D., Tian, L., Looger, L.L., Tank, D.W., 2010. Functional imaging of hippocampal place cells at cellular resolution during virtual navigation. *Nat. Neurosci.* 13 (11), 1433–1440.
- Fassihi, A., Akrami, A., Esmaili, V., Diamond, M.E., 2014. Tactile perception and working memory in rats and humans. *Proc. Natl. Acad. Sci.* 111 (6), 2331–2336.
- Friston, K., 2010. The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11 (2), 127–138.
- Gamzu, E., Ahissar, E., 2001. Importance of temporal cues for tactile spatial-frequency discrimination. *J. Neurosci.* 21 (18), 7416–7427.
- Gibson, J.J., 1962. Observations on active touch. *Psychol. Rev.* 69, 477–491.
- Heiligenberg, W., 1991. *Neural Nets in Electric Fish*. MIT Press, Cambridge, MA.
- Held, R., Hein, A., 1963. Movement-produced stimulation in the development of visually guided behavior. *J. Comp. Physiol. Psychol.* 56 (5), 872.
- Horev, G., Saig, A., Knutsen, P.M., Pietr, M., Yu, C., Ahissar, E., 2011. Motor-sensory convergence in object localization: a comparative study in rats and humans. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 366 (1581), 3070–3076.
- Hubel, D.H., Wiesel, T.N., 1962. Receptive fields, binocular interaction and functional architecture in the cat visual cortex. *J. Physiol.* 160, 106–154.
- James, W., 1890. *The Principles of Psychology*. Holt, Reinhart and Winston, New York.
- Jarvilehto, T., 1999. The theory of the organism-environment system: III. Role of efferent influences on receptors in the formation of knowledge. *Integr. Physiol. Behav. Sci.* 34 (2), 90–100.
- Jun, J.J., Longtin, A., Maler, L., 2014. Long-term behavioral tracking of freely swimming weakly electric fish. *J. Vis. Exp.* 85, e50962.
- Keller, G.B., Bonhoeffer, T., Hübener, M., 2012. Sensorimotor mismatch signals in primary visual cortex of the behaving mouse. *Neuron* 74 (5), 809–815.
- Kelso, J.S., 1997. *Dynamic Patterns: The Self-Organization of Brain and Behavior*. MIT Press, Cambridge, MA.
- Kleinfeld, D., Ahissar, E., Diamond, M.E., 2006. Active sensation: insights from the rodent vibrissa sensorimotor system. *Curr. Opin. Neurobiol.* 16 (4), 435–444.
- Knutsen, P.M., Derdikman, D., Ahissar, E., 2005. Tracking whisker and head movements in unrestrained behaving rodents. *J. Neurophysiol.* 93 (4), 2294–2301.
- Knutsen, P.M., Pietr, M., Ahissar, E., 2006. Haptic object localization in the vibrissal system: behavior and performance. *J. Neurosci.* 26 (33), 8451–8464.
- Konig, P., Luksch, H., 1998. Active sensing—closing multiple loops. *Z. Naturforsch. C* 53 (7–8), 542–549.
- Land, M.F., 2006. Eye movements and the control of actions in everyday life. *Prog. Retin. Eye Res.* 25 (3), 296–324.

- Lederman, S.J., Klatzky, R.L., 1987. Hand movements: a window into haptic object recognition. *Cogn. Psychol.* 19 (3), 342–368.
- Marom, S., 2010. Neural timescales or lack thereof. *Prog. Neurobiol.* 90 (1), 16–28.
- Marom, S., 2015. *Science, Psychoanalysis, and the Brain*. Cambridge University Press, Cambridge.
- Marom, S., Wallach, A., 2011. Relational dynamics in perception: impacts on trial-to-trial variation. *Front. Comput. Neurosci.* 5, 16.
- Marr, D., 1982. *Vision*. W. H. Freeman, San Francisco, CA.
- McDermott, J.H., Schemitsch, M., Simoncelli, E.P., 2013. Summary statistics in auditory perception. *Nat. Neurosci.* 16 (4), 493–498.
- Micheyl, C., Xiao, L., Oxenham, A.J., 2012. Characterizing the dependence of pure-tone frequency difference limens on frequency, duration, and level. *Hear. Res.* 292 (1), 1–13.
- Mountcastle, V.B., Lynch, J., Georgopoulos, A., Sakata, H., Acuna, C., 1975. Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J. Neurophysiol.* 38 (4), 871–908.
- Noble, D., 2008. *The Music of Life: Biology Beyond Genes*. Oxford University Press, Oxford.
- O’Keefe, J., Dostrovsky, J., 1971. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res.* 34 (1), 171–175.
- Oram, T., Ahissar, E., Yizhar, O., 2015. Head-motion modulation of the activity of optogenetically tagged neurons in the vibrissal thalamus. In: Paper Presented at the SfN Annual Meeting, Chicago.
- O’Regan, J.K., Noe, A., 2001. A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* 24 (5), 939–973, discussion 973–1031.
- Packer, O., Williams, D.R., 1992. Blurring by fixational eye movements. *Vis. Res.* 32, 1931–1939.
- Port, R.F., Van Gelder, T., 1995. *Mind as Motion: Explorations in the Dynamics of Cognition*. MIT Press, Cambridge, MA.
- Powers, W.T., 1973. Feedback: beyond behaviorism. *Science* 179 (71), 351–356.
- Prescott, T.J., Diamond, M.E., Wing, A.M., 2011. Active touch sensing. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 366 (1581), 2989–2995.
- Romo, R., Salinas, E., 2003. Flutter discrimination: neural codes, perception, memory and decision making. *Nat. Rev. Neurosci.* 4 (3), 203–218.
- Rosen, R., 1991. *Life Itself: A Comprehensive Inquiry into the Nature, Origin, and Fabrication of Life*. Columbia University Press, New York.
- Rucci, M., Iovin, R., Poletti, M., Santini, F., 2007. Miniature eye movements enhance fine spatial detail. *Nature* 447 (7146), 851–854.
- Saig, A., Gordon, G., Assa, E., Arieli, A., Ahissar, E., 2012. Motor-sensory confluence in tactile perception. *J. Neurosci.* 32 (40), 14022–14032.
- Saraf-Sinik, I., Assa, E., Ahissar, E., 2015. Motion makes sense: an adaptive motor-sensory strategy underlies the perception of object location in rats. *J. Neurosci.* 35 (23), 8777–8789.
- Schroeder, C.E., Wilson, D.A., Radman, T., Scharfman, H., Lakatos, P., 2010. Dynamics of active sensing and perceptual selection. *Curr. Opin. Neurobiol.* 20 (2), 172–176.
- Shahaf, G., Eytan, D., Gal, A., Kermany, E., Lyakhov, V., Zrenner, C., et al., 2008. Order-based representation in random networks of cortical neurons. *PLoS Comput. Biol.* 4 (11), e1000228.
- Simony, E., Bagdasarian, K., Herfst, L., Brecht, M., Ahissar, E., Golomb, D., 2010. Temporal and spatial characteristics of vibrissa responses to motor commands. *J. Neurosci.* 30 (26), 8935–8952.
- Szwed, M., Bagdasarian, K., Ahissar, E., 2003. Encoding of vibrissal active touch. *Neuron* 40 (3), 621–630.
- Tammero, L.F., Dickinson, M.H., 2002. Collision-avoidance and landing responses are mediated by separate pathways in the fruit fly, *Drosophila melanogaster*. *J. Exp. Biol.* 205 (18), 2785–2798.
- Tanaka, Y., Tiest, W.M.B., Kappers, A.M., Sano, A., 2014. Contact force and scanning velocity during active roughness perception. *PLoS ONE* 9 (3), e93363.
- Wallach, A., Bagdasarian, K., Ahissar, E., 2016. On-going computation of whisking phase by mechanoreceptors. *Nat. Neurosci.* 19 (3), 487–493.
- Wiener, N., 1949. *Cybernetics*. John Wiley & Sons, New York.
- Wu, C.-T., Crouzet, S.M., Thorpe, S.J., Fabre-Thorpe, M., 2014. At 120 msec you can spot the animal but you don’t yet know it’s a dog. *J. Cogn. Neurosci.* 27 (1), 141–149.
- Yarbus, A.L., 1967. *Eye Movements and Vision*. Plenum, New York.
- Yartsev, M.M., Ulanovsky, N., 2013. Representation of three-dimensional space in the hippocampus of flying bats. *Science* 340 (6130), 367–372.