32 The Representation of Action

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ABSTRACT   This chapter examines how goal-directed actions are organized from a cognitive perspective. Actions are characterized at a behavioral, cognitive, and structural level within the central nervous system. Three broad approaches are reviewed: context-guided, ideomotor, and process models of action. Context-guided models are a generalization of stimulus-response mapping, embedded in a context that dictates task demands. Ideomotor models begin with a task goal that leads to the retrieval of action memory. Process models focus on constraints associated with action representation: how is information transformed, and how does that influence performance? Together, these approaches provide complementary insight into the organization of complex behavior.

Our ability to manipulate the environment with our hands is a remarkable evolutionary achievement. An everyday task such as tying one's shoes demands exquisite coordination between the hands. This action requires complex, integrative movements of the two hands. Moreover, there must be sufficient flexibility to allow for contextual variations, such as the stiffness of the laces, desired tightness of the shoes, or reorientation of the action, for example tying someone else's shoes. Dexterous behavior is readily accomplished with minimal thought of the procedures to perform the task or the eventual outcome of the action (Bernstein, 1967).

A fundamental problem in neuroscience is to understand goal-directed behavior in terms of the underlying cognitive structure and to link this to neural implementation. This remains a difficult problem because of the motor system's ability to create new motor combinations, to use varied implementations, and to adapt an action representation in response to a changing environment. To date there is no comprehensive model that adequately accounts for action representation. However, by examining a set of contemporary cognitive models for action representation, we can develop a perspective on the overall problem. In this chapter three broad cognitive approaches are reviewed: context-guided, ideomotor, and process models. The first two approaches provide basic insights into how actions are represented. Process models focus on constraints associated with these representations: how is information transformed, and

how does that influence performance? Although the chapter is organized around the different approaches, they overlap in substantial ways and therefore should be viewed as complementary.

Context-guided models

In context-guided models, action representations are linked to specific environmental stimuli. There is a long-standing tradition of viewing an action as a response to a stimulus. In this setting, action formation is a reaction to an external cause. This level of analysis can be traced to Descartes, who first defined actions in terms of perceptual events (Descartes, 1664). The subsequent emergence of experimental methods that largely relied on reaction time measurements allowed action to be explained in terms of the physical properties of stimuli (Donders, 1862 [1969]), and with the emergence of behaviorism this became the dominant paradigm in psychology. This approach facilitated the rapid advancement of theories of performance in which complex sets of stimuli and responses could be functionally linked by simple associative principles.

An important departure from strict behaviorism was to consider the stimulus-response pairing as more than a mapping or rule between input and output. This mapping, together with the context, could be considered as an action representation. Context-guided action-perception pairings are ubiquitous. We depress the brake pedal for a red light and the accelerator for a green light not because the colors demand these actions but because these arbitrary symbols have become associated with certain behavioral goals, such as avoiding collisions. In terms of implementation, at the cellular level there is clear evidence for neurons in the dorsal premotor cortex of nonhuman primate that map arbitrary stimuli to limb movements (Wise, Weinrich, and Mauritz, 1983) and more generally map body parts to objects and locations (Hoshi and Tanji, 2000). Premotor neurons in the monkey show learning-related changes in activity over time as a contextually guided association is acquired (Mitz, Godschalk, and Wise, 1991). Lesions of this area of premotor cortex in humans lead to an impairment in learning new visuomotor associations, such as making a gesture in response to a spatial or color cue (Halsband and Freund, 1990).

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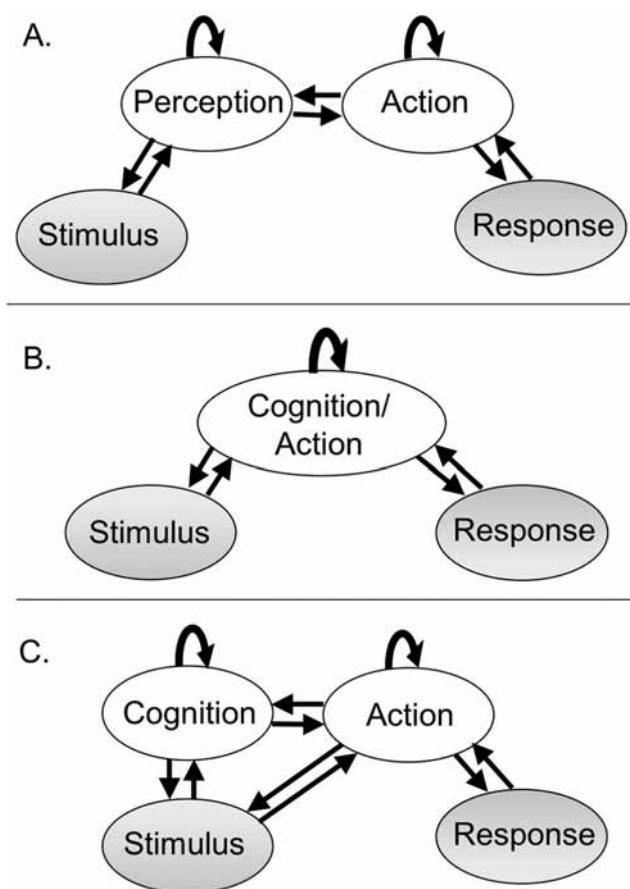RICHARD B. IVRY   Department of Psychology, University of California at Berkeley, Berkeley, Calif.

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FIGURE 32.1. Different formulations of the perception-action interface. In *A*, perception and action are considered separable. In *B*, action and cognition are embodied in the same representational structure. In *C*, there is a direct path from stimuli to action and an indirect path via cognition, which is separable from action.

The notion of context-guided representation is important because it allows us to ask what is actually being represented (figure 32.1). Behavioral studies are inconclusive in determining if context-guided representations are formed with respect to the perceptual features of the task, the movements themselves, or some commonly coded representational structure. Physiological data also underscore the challenge of identifying specific representational structures. At the neuronal level there appears to be no evidence for a unitary representational structure for action. Within a single neuron it is possible to identify perceptual-based, response-based, and combined sensorimotor firing patterns. For example, when a monkey is trained to make pointing movements with a joystick in response to visual cues, many dorsal premotor neurons have increased firing rates to either the location of the instructional cue or the direction of the desired limb movement. However, there are also cells demonstrating both location and direction coding at different times within a single behavioral trial (Shen and Alexander, 1997).

An important aspect of context-guided actions is the reference frame used to define that representation. When we reach for our shoelaces, do we relate the location of the laces in allocentric or egocentric space? If egocentric, is the reference frame defined with respect to the eyes, the hand, the joints required to achieve the action, or some combination of these (see, e.g., Soechting and Flanders, 1992)? How are transformations achieved from one reference frame to another in the perception-action cycle? Physiological recordings suggest a multiplicity of reference frames within common regions of the parietal lobe (Colby, 1998). This proximity allows for the sharing and transformation of information across frames of reference. Anatomical projections from parietal to premotor areas provide information on the current state of the system and the external environment, represented in one or perhaps many frames of reference.

At the output level the limb must ultimately generate a useful movement. In terms of representation, we again need to consider whether movements are defined in an intrinsic or extrinsic coordinate system. Do we move the limb to achieve particular trajectories or final limb configurations, or at a level independent of kinematics in which we achieve a final goal location? Irrespective of the coordinate system used, how does the system accommodate changes of limb dynamics? Our ability to respond to contextual changes is evident when we succeed in tying our shoes even when wearing gloves on a wintry day, or in altering the force of our actions if we see that the lace is frayed.

By altering the dynamics in experimental settings, these problems become tangible. For example, when subjects learn to control the position of a cursor by moving a joystick that has a complex force field applied to it, learning, when assessed by altering the postural configuration of the limb, occurs in an intrinsic, muscle-centered coordinate frame (Shadmehr and Moussavi, 2000). However, after training with one arm, transfer is found only when the altered dynamics are preserved in terms of an extrinsic frame of reference (Criscimagna-Hemminger et al., 2003). Interestingly, there is no transfer if training is completed in the nondominant hand and transfer is to the dominant hand. This observation suggests that the representation accessed following intermanual transfer is generated in the dominant hemisphere and may be distinct from the representation that controls performance when the same limb is used but in another context.

Studies of sequence learning provide an impressive demonstration of the context dependency of stimulus-response associations. On the serial reaction time task (Nissen, Willingham, and Hartman, 1989), subjects press four individual keys with the fingers in response to spatially distinct visual cues. If the order of the cues is presented in a repeating pattern, for example a 12-element sequence, implicit learning is measured by the reduction in response

times relative to blocks in which the stimulus sequence is set randomly. In this type of sequence learning there is typically good transfer across responses systems (Keele et al., 1995). If representational structures were strictly dichotomous, one would conclude that learning is perceptual. However, if the stimulus-response mapping used during training is incompatible, poor transfer is observed following a condition in which a compatible stimulus-response mapping is introduced and the transfer sequence involves a new response sequence but retains the original perceptual sequence (Willingham, 1999; Willingham et al., 2000). Under these conditions, transfer is observed when the response sequence remains invariant, even though this introduces a new stimulus sequence. Thus, the form of representation is likely dependent on task demands.

There is evidence that the level of representation in sequence learning changes over the time course of the training (Bapi and Doya, 1998; Bapi, Doya, and Harner, 2000; Koch and Hoffmann, 2000). For example, early in training, learning may be primarily related to the ordering of perceptual events and the formation of successive stimulus-response associations. With prolonged practice and repetition, learning appears to shift to a response-based level of representation (Karni et al., 1998; Rand et al., 2000). With enough practice we have the capacity to make highly specific, automated movements irrespective of perceptual instructions, and the degree of transfer to other response systems is reduced. Imaging studies of sequence learning demonstrate that retrieval of sequential structure at the response level of representation involves premotor areas in the medial wall of the superior frontal gyrus, including the supplementary motor area (SMA) and adjacent pre-SMA (Gerloff et al., 1997; Shima and Tanji, 2000; Bischoff-Grethe et al., 2003) (figure 32.2).

The preceding discussion suggests that the duration of training or context in which sequence acquisition takes place may constrain the level of representation. However, the form of representation is unlikely to simply reflect the level of expertise. Learning may be perceptual, effector-specific, or goal-based, related to the environmental consequences of the task (Hazeltine, 2002). Moreover, multiple forms of representation may emerge over the course of learning, reflecting constraints associated with different associative mechanisms. Context-dependent representations may require access to inputs from multiple sources, whereas more modular representations may be formed within stimulus-response channels (Keele et al., 2003).

Context-guided learning models are closely related to reinforcement learning algorithms where there is an iterative rule and some form of credit assignment leading to a change in the response (Sutton and Barto, 1998). The credit assignment need not be tied to a specific goal or distal effect. The flexibility of reinforcement learning allows for both supervised and unsupervised forms of learning and includes instrumental conditioning and paired associative learning. When we learn to tie our shoes, we perform thousands of iterations. Unlike reinforcement learning, however, the final goal is not experienced prior to its eventual achievement. Context-guided learning is insufficient for this sort of circumstance, in which there is (1) no predefined mapping or (2) the need to create an entirely new type of response. A comprehensive motor learning model would need to include generative processes for creating novel sensorimotor mapping rules and new forms of motor output.

Context-guided models allow one to consider how actions are selected in a world in which simultaneous inputs provide sources of convergence and competition for the selection of actions, suggesting a need for some form of control system, at least when performing in novel contexts or under conditions in which habitual behaviors are nonoptimal (Shallice et al., 1989). The importance of such control is demonstrated by certain clinical syndromes. Patients with inferior frontal lesions can develop pathological utilization behavior such that their actions are dictated completely by a salient
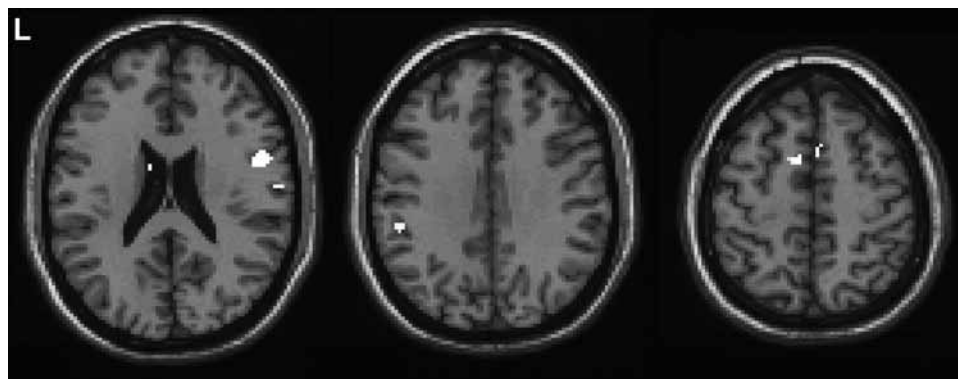

FIGURE 32.2. Functional localization of sequential action retrieval. As subjects perform an implicit sequential task, there is activation of the right ventral premotor cortex (left panel), left inferior parietal cortex (middle panel), and bilateral SMA (right panel) specific to the pattern of responses. Image left is left brain. (Adapted from Bischoff-Grethe et al., 2003.)

stimulus, even when highly inappropriate. For example, when three sets of eyeglasses were presented on the table, a patient proceeded to put them all on, one over the other (Lhermitte, 1983, 1986; Lhermitte, Pillon, and Serdaru, 1986). Slavery to stimulus-bound responses is also observed in the checking behavior exhibited by patients with obsessive-compulsive disorder (Ridley, 1994).

Ideomotor models

Ideomotor models seek to characterize the representation of action based on internal, volitional causes of action. In contrast to context-dependent models, they tend to ignore sensory causes. Actions emerge from internal mental operations rather than external triggers. A major advantage of the ideomotor approach is the formalization of a goal as a causal determinant. As such, ideomotor models work backward in time, with the goal defined initially, followed by a characterization of the implementation processes needed to achieve that goal. Early characterizations of the internal causes for actions were based in large part on self-introspection (James, 1890). Backward causation was first addressed by making a distinction between the goal state itself (a result of an action) and its cognitive representation (linked to the causal implementation).

Ideomotor models of action representation are historically based on findings in patients with apraxia. Apraxia is a disturbance of goal-directed motor behavior that is characterized by an inability to perform previously learned movements in the absence of weakness or sensory defects (Leiguarda and Marsden, 2000). For example, a patient asked to gesture how she would use a comb might fumble with her hand, tapping her head with a fist. Or she might use her fingers as a comb rather than miming gripping an imaginary comb. Success on tasks used to assess apraxia typically requires that the patient identify the action associated with a tool, access the appropriate movement representations, and implement the correct action. In addition, if the object is not presented or modeled, the patient must process linguistic stimuli in order to identify the test object.

Apraxia is more common and severe following left hemisphere lesions than following right hemisphere lesions (De Renzi, Motti, and Nichelli, 1980; Haaland, Harrington, and Knight, 2000). A left hemisphere specialization for action representation is supported by imaging studies showing activation of this hemisphere during action retrieval linked to tool use (figure 32.3). There is also greater left hemispheric involvement for sequential learning with either hand (Grafton, Hazeltine, and Ivry, 2002), as well as asymmetrical patterns of intermanual transfer following training in novel dynamic environments (Grafton, Hazeltine, and Ivry, 2002; Criscimagna-Hemminger et al., 2003).
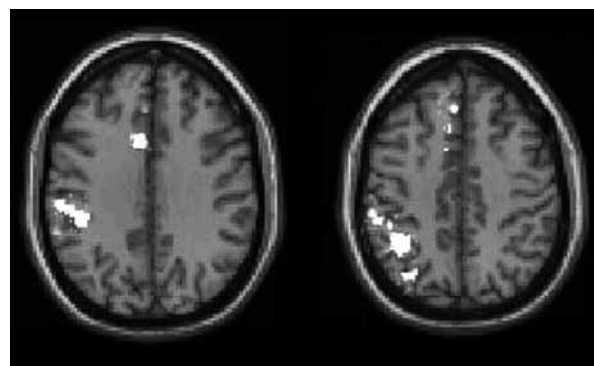

FIGURE 32.3. Common areas of activation among 12 right-handed subjects during gesture retrieval with either the right or left hand. Areas of activation are shown in white at two axial levels spanning the inferior parietal lobule (left section) and intraparietal sulcus (right section). Irrespective of hand, there is consistent activation of the left parietal cortex (image left is left brain).

A recent outgrowth of ideomotor models has been the development of simulation theory (Jeannerod, 2001). The central idea is that mental states of actions involve simulations of the processes associated with the execution of that action. In effect, action and cognition overlap, as shown in figure 32.1B. That is, conceptual knowledge of actions exists through reference to overt actions. Numerous studies have shown the tight linkage between imagined and real actions (e.g., Parsons, 1994; Johnson, 2000). This simulation idea is also supported by functional imaging studies of mental imagery that demonstrate overlap in activation patterns for real, observed, and imagined movements (Sirigu et al., 1995; Decety, 1996; Grafton et al., 1996; Johnson et al., 2001, 2002).

It should be noted that there is only partial overlap of brain areas for these different functions, and in some cases there is a clear distinction between the premotor areas engaged during action ideation and execution (Tyszka et al., 1994; Stephan et al., 1995). It is also not clear if the relationships between ideation, observation, and execution are symmetrical. There is good evidence for motor areas being recruited when we think about action-related concepts (Martin et al., 1995; Barsalou et al., 2003). However, it is not clear that the conceptual areas are recruited for action planning and implementation. Nor is there compelling evidence that lesions of areas associated with action implementation produce deficits in the conceptual knowledge of actions (Heilman, Rothi, and Valenstein, 1982). As will be discussed in the next section, there are many circumstances in which motor selection and control can occur with minimal or no conscious thought.

These patient and imaging studies provide evidence for the distinction between representations for a goal (a distal effect in the future) and the action (the actual implementa-

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tion leading to the goal). However, goal states are elusive, unobservable entities and remain difficult to manipulate experimentally. As a result, a comprehensive conceptual framework for characterizing action goals based entirely on evidence from apraxia patients and imaging of simulated action is incomplete.

Process models

The emphasis in context-dependent and ideomotor models is on the form of action representation. Process models address the same question but through an analysis of the transformation of mental representations. By exploring constraints on actions, a characterization of the representations is possible. For example, in an overlearned task such as shoe tying, the relative timing for each step in the task, such as forming the loops with the laces, remains relatively constant across different contexts. This temporal structure suggests that the action consists of invariant properties that may be associated with invariance due to central mechanisms (Terzuolo and Viviani, 1980) once peripheral causes of invariance are also excluded (Gentner, 1987). Here we examine two process models that reveal insights into how actions are coupled in space and time.

REACH AND GRASP   When we reach and grasp the laces of our shoes, there is remarkable constancy in the timing between the peak acceleration of the reach and the opening of the fingers to match the size of the laces (Jeannerod, 1984). A key point is that the rate of transport is adjusted according to the size of the required hand aperture. This temporal invariance demonstrates the capacity for anticipation within the motor system and reveals that action representation for transport is formed with respect to the demands of the grasping component (Gentilluci et al., 1991). At a more abstract level, anticipation can also be seen in the grasp affordance, that is, the hand orientation and shaping used to grasp the object. The orientation will vary depending on whether we are picking up the laces to tie them or picking up the laces as a means of picking up the shoes (Rosenbaum et al., 1992). Behavioral evidence suggests that the processes associated with reaching and grasping are relatively distinct but interact in specific ways. This has been well-supported in neuropsychological and physiological studies. In both human and nonhuman primates, there is a circuit between the superior parietal lobule and dorsal premotor cortex that is critical for locating the hand in space and central for reaching (Andersen and Zipser, 1988; Caminiti et al., 1991; Andersen et al., 1997; Battaglia-Mayer et al., 2001; Marconi et al., 2001). Lesions of the superior parietal lobule lead to optic ataxia, an impairment of visually guided reaching (Perenin and Vighetto, 1988). Areas specific for grasping are located
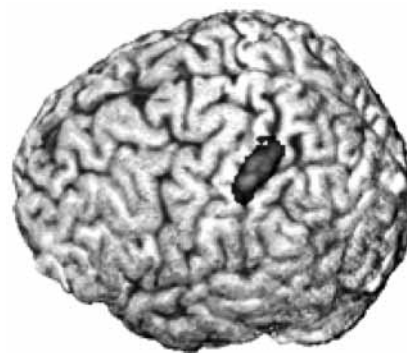

FIGURE 32.4.   Localization of anterior intraparietal activation during contralateral, right-hand grasping compared to pointing in a normal subject. Results are superimposed on a superior oblique view of the left hemisphere.

in the anterior intraparietal sulcus and ventral premotor cortex (Sakata et al., 1992; Jeannerod et al., 1995; Sakata et al., 1995; Murata et al., 2000). Circumscribed lesions of the anterior parietal cortex in humans can lead to deficits in hand shaping, with preservation of arm transport (Binkofski et al., 1998). Grasp-specific areas can also be identified with functional magnetic resonance imaging in normal subjects (figure 32.4). The neural substrates for both reach and grasp lie within the "where" or "how" visual processing stream (Ungerleider and Mishkin, 1982; Goodale et al., 1991).

Another important feature of process models is that motor output can be modified in real time as task goals change. Experimentally, this is demonstrated by perturbing the target during a reach and observing that corrections can occur without vision of the arm and prior to the availability of proprioceptive feedback. Such manipulations presumably mimic the fact that, although targets in a natural environment are usually stable, accurate reaching is impeded by the presence of noise in the motor system (Harris and Wolpert, 1998). To minimize the effects of this noise while sustaining fast, accurate movements, there must be an internal model estimating the current state of the motor system in real time that is available for revising ongoing motor activity. The intraparietal sulcus of the parietal lobe appears to be critical for maintaining and continuously updating an internal representation of the state of the body with respect to the world (Wolpert, Goodbody, and Hussain, 1998; Desmurget et al., 2001). This information would be used for generating error signals based on an efference copy of the motor commands and evolving sensory feedback (Desmurget and Grafton, 2000). Patients with bilateral parietal lesions have difficulty using such an online corrective mechanism, even though their initial reaching movements are relatively spared (Grea et al., 2002). Similarly, transcranial magnetic stimulation of parietal cortex in normal subjects at the onset of a reaching movement will block their ability to update a

reaching movement to a target that has been displaced (Desmurget et al., 1999).

In prehension experiments, many features of the eye and hand movements are produced with minimal influence of cognitive control, and in fact may not be accessible to conscious control. This is evident when one plays sports—rapid body adjustments are executed without our awareness. Unwanted corrections can emerge in patients with parietal lobe lesions. Patients may make online adjustments during reaching movements even when these adjustments are counterproductive toward achieving a motor goal (Pisella et al., 2000). Conscious intervention can also contaminate learned skills under normal conditions. When we try to speed up or slow down a well-learned action such as shoe tying, performance often deteriorates.

Immediate action coding in these circumstances is likely not mediated by the same neural circuitry as action planning for distal effects such as goal selection. Patients may show an inability to consciously perceive or describe sensory information used to generate a motor behavior, but will perform the behavior well under natural conditions. For example, the visual agnosia patient D.F. could not perceive shape or orientation when tested with an explicit perceptual test. However, she could readily "post" an envelope through a slot with the proper hand orientation, a skill that required similar knowledge of orientation and target location (Goodale et al., 1991). This dissociation has been taken to imply that the intact dorsal how pathway allows for unconscious, automatic visually guided actions, including reach and grasp, whereas the damaged ventral what pathway is essential for object recognition and conscious recognition.

An alternative interpretation emphasizes differences in the representations and processes used to guide actions within the dorsal and ventral streams. When patient D.F. indicates the orientation of the object by reaching for the slot, the action is directly specified by the visual stimulus. In the test used to infer conscious knowledge, the action is more symbolic. D.F. observes the slot and attempts to match the orientation of her wrist and the slot without actually reaching. In this condition, the action requires a somewhat arbitrary translation between the stimulus and response, given the symbolic nature of the response.

Bimanual Studies Recent studies on bimanual reaching suggest that there are qualitative differences between actions that are guided by either direct or symbolic representations (Diedrichsen et al., 2001). In these experiments, subjects make two pointing movements on each trial, one with the left hand and one with the right hand. The movement direction for each hand can be forward or sideways. Thus, the bimanual combination is classified as congruent (both forward or both sideways) or incongruent (one forward and one lateral). The critical manipulation centers on the

manner in which the movements are cued (figure 32.5). In the symbolic cuing condition, the four possible target locations (two end locations for each hand) are visible at all times, and the letters F and S indicate the forward and sideways target locations, respectively. One letter is presented in the left visual field to indicate the left-hand movement and the other letter is presented in the right visual field to indicate the right-hand movement. In the direct cuing condition, the target locations are cued by the onset of the target circles, one appearing on each side.

In the symbolic condition, congruent responses are initiated faster than incongruent responses, consistent with previous findings that people show a strong preference for symmetrical bimanual movements. However, when the movements are directly cued, the subjects are much faster to initiate their movements overall, and, more important, congruency has no effect on reaction time. In fact, reaction times on bimanual trials are similar to those obtained on unimanual trials. Thus, the advantage for congruent bimanual actions cannot be attributed to motor programming or execution, as has been typically assumed in the motor control literature (Spijkers and Heuer, 1995; Andres et al., 1999; Cattaert, Semjen, and Summers, 1999; Kilner et al., 2003). These processes should be the same in the symbolic and direct cuing conditions, yet interference is observed only in the former.

The results suggest a distinction in the processes that constrain performance for actions that are symbolically or directly cued. One hypothesis centers on the idea that the two forms of cues result in the action goals being conceptualized in different ways. For symbolically cued actions, the goals are likely represented, at least initially, as abstract spatial codes specifying the desired movement trajectory or path. On congruent trials, these codes would be in correspondence; on incongruent trials, they would be a source of conflict. Not only are there conflicts between the component trajectories required for each hand, but the cues are presented on the left and right sides of the screen and must be assigned to the left and right hands (Diedrichsen et al., 2003). The costs observed on incongruent trials reflects interactions arising due to conflict between the various spatial codes defining the stimulus positions, the required trajectories, and the two hands (Kornblum, Hasbroucq, and Osman, 1990).

In contrast, action goals for directly cued movements are unlikely to be specified in terms of abstract trajectories or movement paths. Rather, the goals are related to the endpoint locations. For direct reaching the degree of conceptual overlap is similar for congruent and incongruent movements. Both require the representation of two distinct locations. The lack of a cost on direct bimanual relative to unimanual trials suggests that the representation of multiple locations can be generated and maintained as well as that of
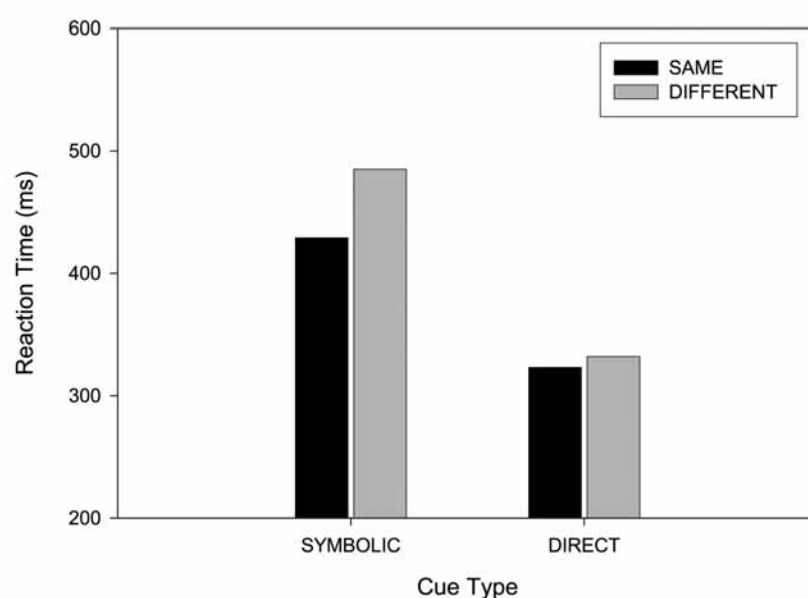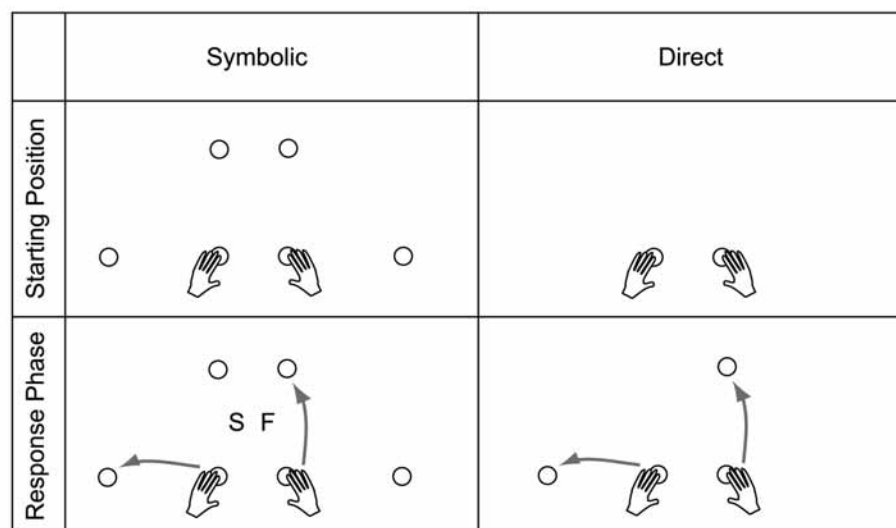
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FIGURE 32.5   *Top:* Method to compare symbolic and direct cuing of reaching movements. Movements were either forward or sideways. In the symbolic condition, the letters F and S cued the required direction for each hand. In the direct condition, two circles appeared, with the location of the left and right circles indicating the target locations for the left and right hand movements, respectively. The movements of the two hands could either be in the same or different directions. The example shows a different direction trial with the arrows schematics of the movement paths. *Bottom:* Reaction times for the four conditions, averaged over the left and right hands. Directly cued movements were much faster and showed no cost on trials requiring movements of different directions. (Adapted from Diedrichsen et al., 2001.)

a single location. It should be noted that for either direct or symbolic actions, the resultant movement requires a translation into a signal that can be used to activate the required muscles. The point here is that the manner in which an action goal is represented, for example in terms of location- or trajectory-based codes, will help define constraints manifest during the performance of these actions.

We can consider an experiment in which three types of action cues were used to define multisegment bimanual movements (J. Diedrichsen, E. Hazeltine, and R. B. Ivry, unpublished observations). The segments formed a three-sided box and the orientation of the boxes for the two hands were either congruent (e.g., both U-shaped boxes) or incongruent (e.g., one U- and one C-shaped box). In the direct reaching condition, two target lights appeared on the table surface, one on the left and the other on the right. The subjects reached to these locations. As soon as their hands entered the target locations, new targets appeared indicating the next locations and the subjects were instructed to continue on to the next pair of targets. In this manner, the subjects produced the three-sided trajectories by moving from one direct cue to the next. In the symbolic condition, the four corners of the boxes were illuminated on the table surface at the beginning of the trial. The target shapes for a given trial were presented on a computer monitor, and the subjects reproduced the shapes on the table surface, moving from one corner to the next. In the third condition, the tracing condition, the four corners of the boxes were again illuminated at the start of the trial. The target shapes were then projected directly on the table, and the participants were asked to simply trace the two shapes simultaneously.

The time to initiate each segment was highly sensitive to the manner in which the actions were cued. The direct reaching condition was much easier than the other two conditions, with the onset times for successive segments on incongruent trials only slightly larger than for congruent trials (e.g., 30 ms increase on initial response time). At the other extreme, initiation times were slower by almost 500 ms in the incongruent condition for the symbolic cues. Of greatest interest was the tracing condition. One might suppose that tracing would be similar to the direct cuing condition, since participants simply had to move along the depicted contours from one target location to the next. However, the initiation times were more than 300 ms longer on incongruent trials than congruent trials. The manner in which the action was represented appears to have been radically changed by presenting the full shape prior to the initiation of the movements. We hypothesize that in the symbolic and tracing conditions, the participants represented the goals as target shapes composed of a series of directional vectors. When represented in this manner, interactions between varying spatial codes occurred and led to interference on incongruent trials.

The distinction between symbolic and directly cued actions suggests computational differences in how information is represented and processed within the dorsal and ventral visual streams. Processing models have emphasized the role of the dorsal stream in visually guided actions, including the representation of target locations and the coordinate transformations required for the translation of sensory information into reference frames useful for action (e.g., Flanders et al., 1992; Cohen and Andersen, 2002). With directly cued actions, the goals need not be abstract, and as such may be subject to the mediating effects of more symbolic representations. For example, it has been hypothesized that these representations are relatively immune to visual illusions associated with object recognition processes. Contrast effects are absent when perceived size is inferred from the aperture of a grasping action or the endpoint location of a pointing response (Goodale, 1998). Correspondingly, the lack of interference on incongruent trials in our bimanual reaching studies suggests that processing within the dorsal stream of each hemisphere is relatively immune to processing within the other hemisphere.

Although the dorsal stream may be sufficient for directly cued movements, symbolically cued movements likely require involvement of more ventral visual pathways. With symbolic cues, ventral areas may be necessary for stimulus identification and the mapping of these representations to appropriate motor output, perhaps in conjunction with premotor cortex. By this hypothesis, symbolically mediated actions entail an additional processing stage, one in which the abstract symbols are mapped onto action codes.

There are a number of reasons why the more abstract operations performed within the ventral pathway might lead to processing constraints not observed with direct actions. Psychologically, response selection processes required for linking abstract stimuli to intended actions have been shown to impose a prominent constraint on multitask performance (Pashler, 1994). This form of interference is especially pronounced for tasks involving overlapping representations, such as the abstract, trajectory-based codes we have associated with symbolically cued actions.

The interactions evident for symbolically cued bimanual movements in neurologically healthy subjects is abolished in split-brain patients (Franz et al., 1996; Eliassen, Baynes, and Gazzaniga, 1999). This suggests that the interactions involve callosal pathways. One possibility is that transcallosal interactions are more prominent for representations within the ventral pathway than for representations within the dorsal pathway. Physiological studies provide indirect support for this conjecture. Receptive field size increases as processing progresses along either the dorsal or ventral pathway. However, a prominent feature of inferotemporal cortex is that these neurons respond to stimuli from either visual field (Ito et al., 1995); thus, the input to these cells must come

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from either hemisphere. Alternatively, the lack of inter-ference for directly cued bimanual movements may reflect reduced representational overlap between such actions. A location-based code entails two distinct target locations for both congruent and incongruent movements.

Recent elaborations of the two-visual-stream model offer a different account of why direct and symbolically cued actions exhibit different forms of constraint. It has been pro-posed that a third stream involving the inferior parietal cortex is sandwiched between the dorsal and ventral streams (Johnson-Frey, 2003). Moreover, this intermediate pathway is hypothesized to be highly lateralized and specialized for actions based on abstract representations and goals (Schluter et al., 1998, 2001). Damage to inferior parietal cortex in the left hemisphere in humans is associated with the most severe forms of apraxia (Heilman, Rothi, and Valenstein, 1982), and imaging studies show pronounced activation of this region for actions requiring the representation of complex object properties, such as when the actions involve the pur-poseful manipulation of tools (Johnson and Grafton, 2002).

Involvement of the left inferior parietal cortex may be essential for actions performed without the affordance of direct cues, that is, for actions planned on the basis of inter-nal goals or symbolic cues. This hypothesis assumes that the computations performed within this region are required for symbolically cued movements produced by either hand. Interference would be expected when a single processor is trying to plan two incompatible actions. As such, inter-ference during bimanual actions would be attributed to a functional hemispheric asymmetry for symbolically cued actions. Directly cued movements are not subject to this con-straint because of a more symmetrical brain organization for regions involved in visually guided actions. An appealing feature of this laterality hypothesis is that it acknowledges the prominent role of the left hemisphere in the representa-tion of complex, abstract actions.

Conclusion

By taking multiple conceptual approaches, it is possible to build a broad perspective on action representations and examine links between psychological constructs and pro-bable neural mechanisms. A recurring observation is that there appears to be no evidence for a unitary frame of reference or representational structure that forms a com-prehensive vocabulary for action representation. Action representations vary as a function of context, construct, and means.

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