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Perception in action: multiple roles of sensory information in action control

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Abstract Perceptual processes play a central role in the planning and control of human voluntary action. Indeed, planning an action is a sensorimotor process operating on sensorimotor units, a process that is based on anticipations of perceptual action effects. I discuss how the underlying sensorimotor units emerge, and how they can be employed to tailor action plans to the goals at hand. I also discuss how even a single action can induce sensorimotor binding, how intentionally implemented short-term associations between stimuli and responses become autonomous, how feature overlap between stimulus events and actions makes them compatible, and why action plans are necessarily incomplete.

Keywords Action effects · Action goals · Event files · Ideomotor · Stimulus-response compatibility

Introduction

A look into a cognitive psychology textbook of your choice would provide a picture of perception and action as two different entities, perception being the faculty that subserves the registration and identification of the cognitive system's input, and action being responsible for producing an appropriate output. Many things are assumed to happen in between, such as matching the input against one's expectations, retrieving some input-related memories, and making a choice between different response alternatives, so that the chapters on perception and action are commonly separated by hundreds of pages. And indeed, this seems to be a reasonable reflection of the role perception and action play in the

still popular stage models of human information processing, which describe the chain of operations the given stimulus undergoes when running through that system. The aim of the present article is to emphasize this point and examine why such a sequential stage view may not always be the most appropriate one when it comes to the relation between perception and action and, in particular, the role perceptual processes play in the planning and control of voluntary, goal-directed action. I shall discuss several ways in which perception contributes to action control, and will briefly sketch the state of the art of the research on this particular topic. Rather than providing a full-fledged review of the literature, I shall restrict myself to pointing out the main principles underlying the diverse types of interactions between perception and action, and illustrate them only by selected empirical findings. However, references to broader treatments of the discussed topics will be provided wherever appropriate.

Action goals and consequences

To introduce one of the major problems in action control and motivation, and to prepare the ground for his favorite ideomotor solution to this problem, James (1890, p. 524) used an example from personal experience:

“We know what it is to get out of bed on a freezing morning in a room without a fire... probably most persons have lain on certain mornings for an hour at a time unable to brace themselves to the resolve... Now how do we ever get up under such circumstances? If I may generalize from my own experience, we more often than not get up without any struggle or decision at all. We suddenly find we have got up. A fortunate lapse of consciousness occurs... the idea flashes across us, ‘Hollo! I must lie here no longer’—an idea which at that lucky instant awakens no contradictory or paralyzing suggestions, and consequently produces immediately its appropriate motor effects”.

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At first sight, this seems to be an example where a goal-directed, voluntary action is carried out without any obvious contribution from sensory information. Indeed, there does not seem to be any external stimulus that eventually moved the agent out of bed. Hence, if there was a triggering stimulus involved, it must have been generated internally. According to James, the action was triggered by what he calls the “representation of the movement”, that is, by thinking of the movement underlying the action in the absence of other, movement-inconsistent thoughts. However, thinking of a movement necessarily involves sensory representations, as all that we can think of for a movement is how it feels or looks or sounds to perform it. In other words, our only conscious access to the movements of our own body is mediated by our senses—we know our actions from self-perception.

This line of reasoning has led to what has come to be known as ideomotor theory. Whereas early ideomotor theorists have focused on the issue of how consciousness can acquire and exert control over the human body (for overviews, see Prinz 1987; Stock and Stock 2004), modern approaches are more interested in the functional and brain mechanisms underlying ideomotor control in general (Greenwald 1970; Hommel et al. 2001a; Jackson and Decety 2004; Prinz 1990; Rizzolatti et al. 2001), and the cognitive and cortical representation of action in particular (Elsner and Hommel 2001; Elsner et al. 2002; Hommel 1997). If it is true that the cognitive access to action control is mediated by perception (i.e., by making use of codes that represent past perceptions and anticipations built thereupon), we need to assume that the codes and processes that are responsible for setting up and executing a particular action are linked to codes that represent the perceptual aspects of this action.

However, action codes are not unitary structures, as the primate brain represents actions in a distributed fashion. For instance, distinct cell assemblies in different brain areas code the direction (Georgopoulos 1990), force (Kalaska and Hyde 1985), and distance (Riehle and Requin 1989) of an arm movement, and the coding of each of these parameters gives rise to distinct electrophysiological brain patterns (e.g., Bonnet and MacKay 1989; Kutas and Donchin 1980; Vidal et al. 1991). Accordingly, an action plan must be understood as an assembly of codes that specify the different features the planned action is supposed to have. From an ideomotor perspective, this implies that a code specifying the particular movement parameter is associated with, and accessed and retrieved via codes derived from the perception of the specific movement characteristic this movement parameter is responsible for. For instance, the parameter that specifies the forward direction of a movement must be associated with a code mediating the perception of a forward movement, and the same applies to any other movement parameter. In other words, the structures that mediate voluntary control over the features of our action are sensorimotor units or mini assemblies—units or assemblies with a

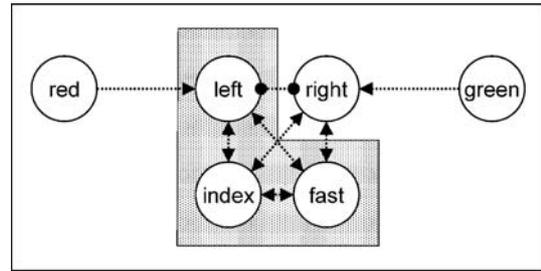


Fig. 1 Basic structure of the cognitive codes underlying a binary-choice reaction-time task requiring a speeded response with the left index finger to red stimuli and a speeded response with the right index finger to green stimuli. The left response is represented by a binding of the relevant codes $\langle \text{left} \rangle$, $\langle \text{index (finger)} \rangle$, and $\langle \text{fast} \rangle$ (see shaded area), triggered by activation of the code $\langle \text{red} \rangle$. Note that the response-discriminating codes $\langle \text{left} \rangle$ and $\langle \text{right} \rangle$ inhibit each other

function in both perception and action planning (Hommel 1997; Hommel et al. 2001a).

Figure 1 provides an example for how these considerations apply to a simple binary-choice reaction-time task. Assume you are presented with red and green stimuli, and are to carry out a speeded response with your left versus right index finger, respectively. Minimally, a given movement has thus three features: it is carried out with a particular hand, with a particular finger, and it is carried out fast. Accordingly, the plan to carry out a left response would comprise the three codes $\langle \text{left} \rangle$, $\langle \text{index} \rangle$, and $\langle \text{fast} \rangle$, which are integrated into a temporary assembly, indicated in the figure by the shaded area. Likewise, the plan to carry out the right response would comprise of the codes $\langle \text{right} \rangle$, $\langle \text{index} \rangle$, and $\langle \text{fast} \rangle$ (assembly not indicated in the figure). Note that in this particular example, two codes are shared by the two assemblies (a situation that is known to create some degree of coding conflict: Stoet and Hommel 1999), so that only location codes discriminate between the two responses. If we assume a capacity limitation with respect to the number of assemblies that can be active at the same kind, activating one assembly must inhibit any other, as indicated by the inhibitory relation between $\langle \text{left} \rangle$ and $\langle \text{right} \rangle$ in the figure¹. To implement the relevant stimulus-response mappings, each of the two location codes is associated with the corresponding color code via a short-term link, so that a stimulus that activates one of the color codes would automatically prime one of the responses.

¹James (1890) extended this limited-capacity logic to explain how activated action plans (i.e., the actions one “thinks of”) can be held in check: thinking of an action may indeed prime corresponding motor structures to a degree that triggers its execution *unless* one manages to think of another action that is incompatible with it. However, there is a theoretical alternative to this inhibitory control strategy: the execution of an action may not only require a worked-out plan to be carried out but also a go signal to eventually trigger the execution (Bullock and Grossberg 1988). Indeed, evidence from dual-task studies suggests that planning and executing an action are dissociable processes (De Jong 1993; Ivry et al. 1998; Logan and Burkell 1986).

Before getting to the consequences of bringing an external stimulus into play, let us first consider for a moment the action plan as such. As pointed out, it is an assembly of codes that by themselves are sensorimotor structures, so that they have a dual potentiality by representing a sensory event (the experience of something fast, performed by the left or right index finger) and by controlling the production of the corresponding sensory event (i.e., the action). This dual potentiality renders action planning an *anticipatory* process, a process that necessarily takes into account the perceptual qualities of the to-be-produced action effects. And indeed, it is these sorts of action effects that actions are aimed at: you want to produce something fast by using the left index finger because this communicates to the experimenter that you have seen the red stimulus.

Early ideomotor approaches have been either restricted themselves, or were interpreted as being restricted, to what one may call *proximal* effects of actions. If we take the left-finger movement, proximal effects would comprise the kinesthetic experience of moving the finger and the tactile experience of touching the end position but not, say, the perception of a light that is switched on by a finger movement or of a feedback message on a screen. And yet, James (1890) already pointed out that there is no reason to exclude such remote or *distal* effects from ideomotor logic. This becomes particularly obvious if we consider the acquisition of ideomotor links. In order to generate an ideomotor database, we need a learning mechanism with two characteristics.

First, the mechanism must be able to integrate the motor codes that are or just were actively involved in producing a particular action with the perceptual events that follow. At least two learning principles must underlie this integration: contiguity and contingency (Elsner and Hommel 2004). Temporal contiguity is important because the integration mechanism cannot know in advance what might count as a plausible action effect. Thus, it must use a particular temporal integration window and accept for integration any event that follows the action within a particular interval. Obviously, such a mechanism would favor proximal effects, as these commonly occur immediately, but it would have no means to exclude more distal effects—if they only occur in time. Contingency is important to exclude spurious events that may incidentally fall into the integration interval. That is, with increasing experience, only those events should remain integrated with an action that are actually produced by (i.e., are contingent on) it.

A second characteristic that the learning mechanism must comprise is that it needs to create *bidirectional* associations. This directly follows from the fact that using an association between an action and its effects necessarily reverses the order of events experienced when learning the association. That is, whereas we learned that moving the left index finger is followed by the experience of something we feel “in” (or attribute to)

our left index finger—which implies a motor-sensory sequence—we later make use of the association that emerged by activating the sensory code (the “anticipation”) to prime the motor code—a sensorimotor sequence.

There is ample evidence that a learning mechanism with exactly these two characteristics does indeed exist. One way to demonstrate this is to present people with novel, distal events that are contingent on their actions. If this would lead to the creation of bidirectional associations between the motor codes of the action and the sensory codes of the new events ($m \leftrightarrow s$), stimuli that are similar to, or identical to these new events should become effective primes of the corresponding action ($s \rightarrow m$). Consistent with this prediction, high and low tones that were previously produced by pressing left and right keys, respectively, were found to turn into primes of the response they had previously followed (Hommel 1996). Likewise, facing particular action-effect sequences ($m_1 \rightarrow s_1, m_2 \rightarrow s_2$) facilitates the later acquisition of a stimulus-response mapping that heeds the resulting relations ($s_1 \rightarrow m_1, s_2 \rightarrow m_2$) rather than a mapping that does not ($s_1 \rightarrow m_2, s_2 \rightarrow m_1$; Elsner and Hommel 2001). That is, stimuli that were experienced as action effects acquire the potential to activate the action they had previously followed. That they do so in a rather automatic fashion is suggested by a recent PET study, where the mere presentation of previously acquired, auditory action effects was found to activate motor structures (in the caudal supplementary motor area) in a passive tone-monitoring task (Elsner et al. 2002). Action-effect learning seems to be a rather general phenomenon, as effective learning has been demonstrated not only for auditory stimuli but also for visual location (Hommel 1993), visual letters (Ziessler and Nattkemper 2002) and words (Hommel et al. 2003), or the affective valence of visual (Caessens et al., submitted) and electrocutaneous (Beckers et al. 2002) feedback.

Learning studies of this sort demonstrate that both proximal and distal action effects become integrated with the responses they follow. However, more evidence is needed to show that action effects really play a role in action control. Evidence of this type is provided by studies that demonstrate effects of the compatibility between “natural” (or already acquired) action effects and novel, experimentally induced effects of the same action. For instance, subjects were shown to be faster if the spatial relationship between a response (i.e., finger and key location) and a novel, visual effect was compatible (i.e., the relative spatial locations of visual effect and response matched) rather than incompatible (i.e., the relative spatial location of visual effect and response did not match; Hommel 1993; Kunde 2001). As the action effects did not function as primes here (i.e., all effects always followed their responses), these findings indicate that selecting an action must have involved the anticipation of action effects (i.e., the activation of action-effect codes) at some point in the process of selecting a response.

In summary, planning and carrying out a goal-directed action are likely to involve sensory information or, more precisely, anticipation of to-be-expected sensory consequences of the planned action. Referring back to William James and his problem of getting out of bed, a successful solution was likely to involve the anticipation and comparison of the consequences of getting up versus staying in bed the whole day; this does not necessarily imply any conscious decision-making—any direct or indirect activation of the codes of the relevant action effects will do, just think of looking at a clock and the forthcoming associations (“I will be too late, miss the bus”, etc.).

Event files

It is well known that repeatedly responding to a stimulus creates an association between that stimulus and the response. However, there is evidence that even the performance of a single action can leave behind a memory trace connecting the codes of that action with codes of the perceptual context in which it was carried out (Hommel 2004). To take our example from Fig. 1, performing a single movement with the left index finger to a red stimulus will create at least a weak binding between the relevant codes <red> and <left> (see Fig. 2). Before considering why this might be the case, let us first look at the evidence suggesting that binding does take place.

Consider a sequence of two stimulus-response episodes, a previously cued and prepared manual (left-right) response R1 to the mere onset of a visual stimulus S1, followed by another manual (left-right) response R2 to the shape, say, of another visual stimulus S2. Given that R1 does not depend on the shape of S1, such a design can be used to independently vary the match between the shapes of S1 and S2, and the match between the two responses R1 and R2. As one would expect, repeating both the stimulus and the response yields a very good performance (Hommel 1998a). Surprisingly, however, the no-match condition (i.e., both stimulus and response change) produces a performance that is just as good, whereas reaction time is slowed and errors are more frequent in the two partial-match conditions, that is, if the stimulus repeats while the response does not, or vice versa. Hence, encountering exactly the same stimulus-response situation once more is much less beneficial than facing a partial one, but incomplete replication is detrimental. This is not an isolated finding but the negative impact of partial stimulus-response repetitions has been observed in numerous studies using various tasks (for overviews, see Hommel 2004; Hommel and Colzato 2004).

Observations of this sort suggest that the mere co-occurrence of a stimulus and a response is sufficient to create a binding of the codes of at least the relevant stimulus and response features—an *event file* (Hommel 1998a). Once bound, encountering one of the features

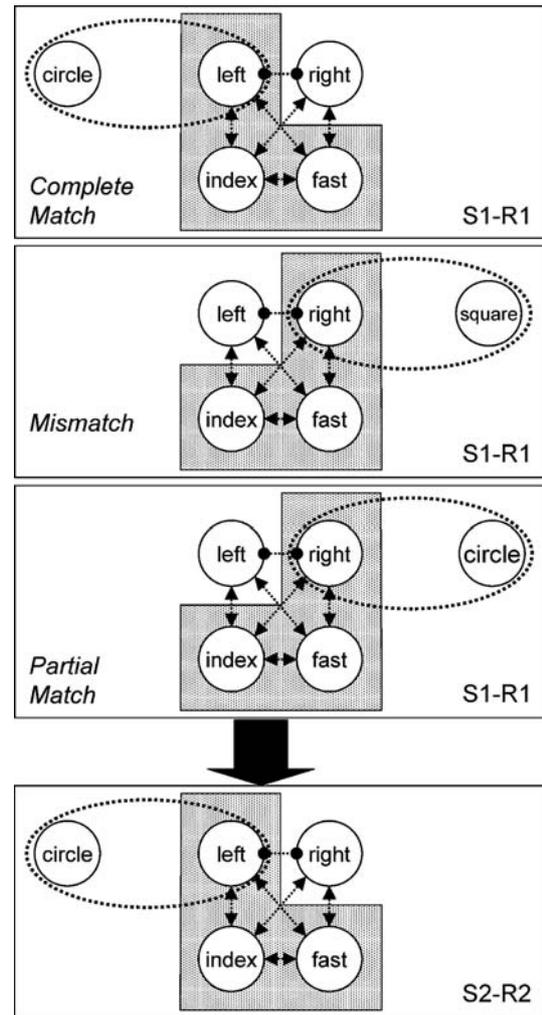


Fig. 2 Explanation of partial overlap costs: the example shows the impact of the accidental binding of a shape stimulus feature (*circle* or *square*) and a left or right index-finger response (*upper three panels, S1–R1*) on the subsequent performance of a speeded left index-finger response to a circle (*bottom panel, S2–R2*). Pairing the shape and the response will lead to a binding between the shape feature and at least the relevant response feature, that is, between <circle> and <left>, <square> and <right>, and <circle> and <right> in the three examples. It is obvious that the third possibility, the partial match condition, will induce a time-costly response conflict: reviewing the circle and activating the corresponding feature code will spread activation to the other member of the binding, in this case, the incorrect and conflicting right response

another time will reactivate its code, which again spreads activation to its previous partners, that is, to the codes it is still bound with. This does not seem to matter much in case of complete match, and no code is reactivated with a complete mismatch anyway. In case of a partial match, however, the code(s) of the repeated feature(s) will prime the code(s) of the non-repeated feature(s) as well, which is likely to create code confusion, thereby hampering stimulus identification and/or response selection (Hommel 2004; see Fig. 2).

Recent findings suggest that what can be bound is not restricted to stimuli and responses but can involve whole

task sets. Waszak et al. 2003) had subjects switch from naming the word component of word-picture compounds to naming the picture component, and vice versa. Not surprisingly, switching the task incurred a cost in terms of reaction time and error rates, as found by many other studies (for an overview, see Monsell 2003). Importantly, however, switching to a task was much more costly if the current stimulus had already been encountered under the other, competing task. That is, the stimulus must have become associated with the previous task, so that seeing the stimulus again tended to reactivate the corresponding task. These kinds of effects can be obtained after a single pairing of a stimulus and a task, and more than 100 trials after the pairing took place.

There are several possible reasons why such effects may occur. One is that we may be tapping into episodic memory, which may automatically record any possible stimulus and response feature present in a given situation (cf. Logan 1988). And, indeed, event files can certainly be considered as episodic memory structures that represent contextualized events. However, there may be another, related but more functionally motivated reason. Given the distributed representation of perceived events and action plans, the human brain constantly faces the problem of defining which belongs to which, including the features of stimuli and responses belonging to the same episode. Integrating all this information into a coherent structure may be an important means to clarify the relevant relations, which among other things is a necessary precondition for creating the most appropriate associations in learning. In other words, integrating features into event files may subserve the creation of cortical processing units, which then provide the raw material for episodic memory.

In any case, the automatic generation of event files contextualizes actions and provides them with stimulus-, context-, and task-specific retrieval cues. These cues allow accessing and activating an action in a bottom-up (i.e., stimulus-driven) or top-down (i.e., goal-driven) fashion.

Short-term associations

When we instruct someone else to carry out a particular stimulus-related action, he or she is commonly able to follow this instruction right away (provided that it already belonged to his or her repertoire), that is, to perform the action without much practice or the necessity to repeat the instruction over and over again. This implies that people are able to translate instructions into short-term associations between the stimulus or stimuli and the responses they require, and to maintain these associations until the task is completed. Recent models of executive control assume that whole task-specific sets of stimulus-response associations can be implemented to configure the cognitive system in a task-specific fashion (e.g., Cohen et al. 1990; Gilbert and Shallice 2002;

Logan and Gordon 2001). In fact, these associative sets are commonly taken to represent the intentions of the acting person or what earlier accounts called the “will” (Ach 1910; James 1890). However, short-term associations have a number of characteristics that do not seem to fit into this picture.

First, they seem to function in an operating mode that Bargh (1989) has coined “conditional automaticity”. That is, even though the *implementation* of short-term stimulus-response associations is commonly intentionally driven, they *operate* in an automatic fashion. A frequently used example is the flanker-compatibility effect first reported by Eriksen and Eriksen (1974). If subjects are to respond to a visual target, they are often unable to ignore close-by distractors. For instance, if a discriminative response is required for a central target letter flanked by distractor letters, performance is better if target and distractors are associated with the same response than with different responses. This implies that distractors have access to stimulus-response rules and are automatically translated into the response they are associated with.

One may attribute this observation to a mere failure of spatial attention, but there are more demonstrations of the automatic use of intentionally created associations. When people switch between tasks that are defined by partially different stimulus-response mappings, their performance is often impaired with stimuli that require different responses in the two tasks. For instance, if one task requires a left and right key press to odd versus even digits, respectively, and the other task a left and right key press to digits lower versus higher than five, performance would be worse on a seven than on a one (Sudevan and Taylor 1987). This implies that each stimulus has access to, and is automatically processed by short-term associations related to both the currently relevant and the currently irrelevant task. The same conclusion is suggested by task-mixing effects on the Simon effect. The Simon effect is observed when people perform spatial responses to a nonspatial feature of a spatially varying stimulus. If, for instance, a left-hand response is signaled by a green and a right-hand response by a red stimulus, the left-hand response will be faster if the green stimulus appears on the left side, whereas the right-hand response will be faster if the red stimulus appears on the right side (Craft and Simon 1970; Simon and Rudell 1967). In other words, the spatial compatibility between stimulus and response facilitates performance even if the stimulus location is entirely irrelevant to the task—an issue to which I will return later on. Interestingly, the size of this effect is strongly affected by mixing the Simon task with a task that renders the stimulus location relevant (Proctor and Vu 2002; Proctor et al. 2003). In particular, if in this other task people respond in a spatially compatible fashion (left responses to left, and right responses to right stimuli), the Simon effect is enhanced, and it is reduced if the other task requires people to respond in a spatially incompatible fashion (left responses to right,

and right responses to left stimuli). This suggests that people are unable to fully separate the different sets of short-term stimulus-response associations needed to perform the two tasks.

Another example is provided by the so-called *backward compatibility* effect in dual tasks. This effect can be observed if people respond to two different features of a stimulus or stimulus display (S1 and S2) by performing two different actions (R1 and R2). Such conditions are known to produce a delay in the second response, a finding that has been attributed to a processing bottleneck related to response selection (Pashler 1994; Welford 1952). Interestingly, however, the first action is affected by its compatibility with the second action (Hommel 1998b; Logan and Schulkind 2000), which suggests that the translation of S2 into R2 takes place parallel to S1–R1 translation. That is, if there is a processing bottleneck in dual task performance, it does not prevent a multiple stimulus-response translation.

A second not so “intentional” characteristic of short-term associations is that they are sticky, that is, they can last longer than they are useful. For instance, backward compatibility effects can be obtained even for responses that are no longer required. Hommel and Eglau (2002) had people perform a manual and a vocal response to the color and shape of a stimulus, respectively. A backward compatibility effect was obtained, that is, the manual response to the color was sped up if the vocal response was compatible with the current color responded to (e.g., the manual key response to a green color was faster if the vocal response was “green”). Then, after a little practice, subjects no longer needed to carry out the vocal response and, yet, the manual response was still faster if it was compatible with the vocal response that was previously mapped onto the current stimulus (e.g., the manual key response to a green color was faster if the no longer necessary vocal response was “green”). Apparently, then, stimuli were still translated into their vocal responses, suggesting that the underlying stimulus-response associations were still active. Similar transfer effects have been observed from tasks in which the spatial relation between stimuli and responses was relevant (i.e., spatially compatible or incompatible) on subsequent tasks in which these relations were not relevant (i.e., Simon tasks). Comparable to the mixing effects mentioned, performing a task with a spatially compatible or incompatible stimulus-response mapping enhances and reduces the size of the Simon effect in a task carried out later on (Proctor and Lu 1999; Tagliabue et al. 2000); under some conditions, these aftereffects survived no less than 7 days (Tagliabue et al. 2000; Vu et al. 2003).

To summarize, once one or more sets of short-term stimulus-response associations are (intentionally) implemented, they, to some degree, live a life of their own and translate any available input into the associated response. Even if they are no longer needed, they at least under some conditions keep translating input into output. Hence, even though the creation of associations is

contingent on the action goal, they operate automatically—a kind of prepared reflex (Hommel 2000).

Long-term associations

It is almost trivial to say that experience shapes our behavior. Obviously, almost all sensorimotor skills require considerable amounts of practice to bring them to and keep them at a certain level, which demonstrates the importance of stable, well-maintained synergies between perception and action systems. The impact of long-term associations on behavior is also visible in the difficulty of getting rid of unwanted or inappropriate stimulus-driven behavioral routines; just think of context-induced drug abuse, addiction, and criminal behavior. However, there are more subtle, less obvious ways in which long-term associations between stimuli and responses or, more precisely, between stimulus codes and response codes shape human action, and it is some of these ways that I would like to consider briefly.

As pointed out above, establishing particular, task-related short-term associations is something that one may call a “controlled” process (e.g., Monsell 2003), but once they are established, such associations can show a rather autonomous behavior. That is, it does not seem to be easy and not always possible to stop them from associating stimuli and responses in a way that directly impacts response selection. Even though they are far from determining which selection is eventually made (suggesting that at least their behavioral effects can be controlled to some degree), they do induce particular response tendencies that support or interfere with the actually intended response. The least we can say is that short-term associations are sticky, in the sense that they live longer than needed. But seeing them survive much longer, such as 7 days, in the studies of Tagliabue et al. (2000) and Vu et al. (2003), raises the question of whether there is any functional difference between short-term and long-term associations. Indeed, approaches like the instance theory of Logan (1988) claim that even a single stimulus-response episode is stored and maintained for an unlimited amount of time. If so, performing a single response to a particular stimulus may be sufficient to increase the tendency to carry out that response to that stimulus again in the however far future. That this is indeed a possibility is suggested by Waszak et al.’s (2003) observation that a single presentation of a stimulus under a competing task is sufficient to make switching to another task more difficult, even if that presentation occurred more than 100 trials earlier. There is still a leap between the about 20 min that this implies and the 7 days observed by Tagliabue et al. (2000) and Vu et al. (2003), but it is remarkable to see such a strong and stable impact of one-trial learning. Observations of this type challenge the traditional distinction between short-term and long-term learning, and they raise the question of how long-lasting the consequences of a single behavioral act can be.

Feature overlap

If perception and action would really be as separated as the linear structure of standard information-processing models seems to make us believe, stimulus characteristics should not interact with response characteristics, and vice versa. And yet, there are numerous observations that particular combinations of stimuli and responses produce much better performances than others, as if some stimuli had a sort of privileged access to, and can be more easily translated into some responses. Most of these observations have been made in three research areas.

First, it has long been known from ergonomic studies that combining stimuli and responses that are somehow similar allows for a faster and more accurate performance (Loveless 1962). For instance, pressing a left versus right key in response to a stimulus presented to the left versus right of a display yields a better performance than responding to two different symbols presented at the center, or by mapping the left key onto the right stimulus and the right key on the left stimulus. Kornblum et al. (1990) have pointed out that two different types of privileged relationships or compatibility between stimuli and responses can be distinguished. *Set-level compatibility* refers to the similarity between the whole stimulus set and the whole response set. For instance, word stimuli and vocal responses or spatial stimuli and location-defined responses are more set-level compatible than color stimuli paired with word responses or word stimuli combined with spatial responses. Likewise, the combination of spatial words and spatial responses can be considered more set-level compatible than the combination of color words and spatial responses. In contrast, *item-level compatibility* refers to the way particular stimuli are mapped onto particular responses. Obviously, item-level compatibility presupposes at least some degree of set-level compatibility, as no combination of items of totally unrelated sets can be considered more compatible or incompatible than another. If sets are compatible, however, one can distinguish compatible stimulus-response pairings (e.g., left response to a left stimulus or the word “left”) and incompatible stimulus-response pairings (e.g., left response to a right stimulus or the word “right”). A particularly interesting characteristic of (item-level) stimulus-response compatibility is that it affects performance even if the respective features are not relevant to the task at hand. The Simon effect mentioned above is one example, and the famous Stroop effect another (Stroop 1935).

Stimulus-response compatibility effects suggest that stimuli directly activate responses they share features with (Kornblum et al. 1990; Prinz 1990). Indeed, by using EEG and brain-imaging techniques, several studies could show that the processing of particular stimulus features activates feature-overlap actions (e.g., Dassonville et al. 2001; Eimer 1995; Liu et al. 2004; Watkins

et al. 2003). As Greenwald (1970) has argued, this observation is expected from ideomotor theory, according to which, responses are represented in terms of the perceptual effects they are likely to produce (see above). A left-hand key press, for instance, produces a couple of perceptual effects and most of them are located on the left side. Accordingly, this key press is likely to be represented by the feature code <left>, among other things. If so, coding the features of a left stimulus would activate the same code that is associated with the left response, which by means of spreading activation should thus be primed. In other words, stimulus-response compatibility would be due to the fact that the same neural codes are used for coding the features that compatible pairings share.

If the ideomotor interpretation of stimulus-response compatibility effects really holds, that is, if stimulus-response compatibility would actually be an effect of the relation between stimulus features and the features of the perceptual consequences of the respective action, one should be able to modify standard compatibility effects by introducing novel action consequences and by pitting them against more “natural” effects. To test that, Hommel (1996, experiment 1) had subjects carry out a nearly standard Simon task: they responded to the color of a visual stimulus by pressing a left or right key. In another block, they performed the same task but now each key press triggered a brief tone on the opposite side. The idea was that pairing each response with an irrelevant, but hardly to be missed action effect on the opposite side should make spatial action coding more equivocal: both left- and right-hand actions had both left- and right-side action effects so that they would be partly compatible and partly incompatible with either stimulus location (see Fig. 3). If so, one would expect the Simon effect to be smaller in the incompatible-tone condition, and this is exactly what was found.

Hommel (1993) went one step further in investigating whether people can be made to selectively attend either the more “natural” action effects or their experimentally induced counterparts. He had subjects react to the pitch of tones by pressing a left- or right-hand key. Pressing a key flashed a light on the opposite side, hence, pressing the left key flashed a right light, and vice versa. That is, the action-effect mapping was spatially incompatible. One group of subjects was instructed in terms of keys to be pressed, that is, they were to “press the left-hand key” in response to a low tone and to “press the right-hand key” in response to a high tone. As expected, these subjects produced a Simon effect, hence, they responded faster if the tone sounded on the same side as the key they needed to press. Another group was instructed in terms of light flashing, that is, they were to “flash the right-hand light” in response to a low tone and to “flash the left-hand light” in response to a high tone. As the right-hand light was flashed by pressing the left-hand key, and vice versa, the task this group carried out was nominally identical. However, if people code their actions in terms of intended action effects, or goals, as the

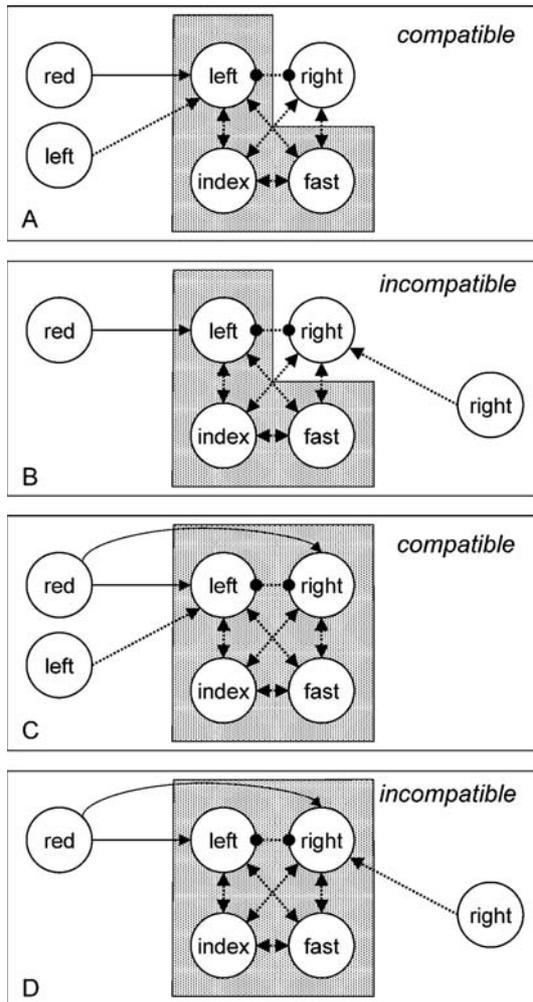


Fig. 3 Basic structure of the cognitive codes underlying the task of Hommel (1996, experiment 1). The stimulus-response mapping requires speeded responses with the left index finger to a red stimulus and with the right index finger to a green stimulus. All four examples assume that the red stimulus appears and the left responses required. **a** shows the compatible condition with the standard Simon set up, that is, the red stimulus appears on the left, response-compatible side. Accordingly, activating <red> triggers the left response binding (as intended) and activating <left> (unintentionally) converges on the same response (actually, the two <left> codes can be considered to be identical). **b** shows the incompatible condition, where the color and the location of the stimulus activate different, competing responses. The relative greater response conflict in the incompatible condition accounts for the Simon effect. **c** and **d** show how the same two conditions are affected by introducing spatially response-incompatible action effects (response-triggered tones on the opposite side of the response key). The response bindings now include (a weaker version of) the code <right>, because the left index-finger response leads to a <right> action effect. As a consequence, the left stimulus is less compatible, and a right stimulus is less incompatible with this response

ideomotor approach implies, subjects in this light-instruction group would be expected to code their actions in terms of the light location (see Fig. 3). If so, the Simon effect should reverse because now a stimulus on the left side would correspond to the (left) goal of the right-hand action and vice versa. Indeed, this is what the

findings show, suggesting that acquiring novel action effects provides a viable alternative to cognitively code one's own actions. To summarize, if stimuli share features with responses or, more precisely, with the perceptual effects these responses produce, they are able to prime these responses, which facilitates response selection in conditions of stimulus-response compatibility but hampers response selection under incompatible conditions.

Most research on stimulus-response compatibility has focused on features that are defined physically (most notably, location but also size, shape, and color on the stimulus side) or semantically (e.g., the relationship between a red stimulus and the vocal response "red"). However, a second line of research suggests that compatibility may also be "pragmatically" defined. In a number of studies, Schubotz and von Cramon (2001, 2002), Schubotz et al. (2000) had subjects monitor streams of visual or auditory events for oddballs, that is, for stimuli violating the otherwise systematic, repetitive structure of the stream. Using fMRI, Schubotz and von Cramon made the surprising observation that premotor areas were heavily involved in this purely perceptual task. Moreover, the areas which were involved depended on the modality or feature dimension of the oddball: the activation within the lateral premotor cortex was highest in areas that are known to be involved in actions that would profit most from information defined in that modality or on that feature dimension. For instance, attending to shape activated a frontoparietal prehension network, attending to location-activated areas involved in manual reaching, and attending to the time pattern activated a network associated with tapping and uttering speech. As the authors suggest, this points to an important integrative role of the human premotor cortex in the anticipation of perceptual events and the control of actions related to these events. More concretely, it may integrate actions and their expected consequences into a kind of habitual pragmatic body map (cf. Schubotz and von Cramon 2003), which would directly embody the main principle of ideomotor theory: actions are represented by codes of their effects. This pragmatic perspective has the potential of adding an interesting Gibsonian dimension to stimulus-response compatibility approaches. Visual shape information and a manual grasp are related in the sense that the former "affords" the latter by specifying the most relevant parameters needed to carry it out (cf. Gibson 1979; Tucker and Ellis 1998).

A third line of research that is taken to suggest some sort of privileged access of some stimuli to some responses is connected with the term "mirror neurons". When Di Pellegrino et al. (1992) measured single-cell activity in the rostral part of the inferior premotor cortex of a macaque monkey, they found that the same cells were active while the monkey was performing particular goal-directed actions himself and while he watched an experimenter doing so. These so-called mirror neurons are particularly sensitive to the

experience of interactions of an agent and a goal object, but insensitive to either objects alone or objectless pantomimes (Gallese et al. 1996). Interesting for present purposes, watching actions activates the human homologue of the indicated area of the macaque brain (Grafton et al. 1996), whereas novel, meaningless movements yield no effect (Decety et al. 1997). Consistent with ideomotor accounts, observing an action primes the same muscle groups that would be used to carry it out (Fadiga et al. 1995). The discovery of mirror neurons continues to provide a source of inspiration for all sorts of speculations on the basis of empathy, human sociability, imitational skills, or the origin of language, and it is fair to say that the richness of these speculations contrasts with the scarcity of available data. What seems obvious, however, is that mirror neurons integrate perceived action effects and motor patterns in a way that makes them promising candidates to mediate effect-based action planning (Miall 2003).

To summarize, available stimulus information can directly impact the selection and performance of actions if it possesses features that physically, semantically, or pragmatically overlap with actions that are considered for selection. From the point of view of action selection, this demonstrates the important role of perceptual anticipations of the consequences of actions in the selection process. From a perceptual point of view, it challenges the widespread assumption that there is such a thing as pure perception. In contrast, action systems seem to be actively involved even in rather simple perceptual tasks, so that we not only perceive what an observed event affords, we to some degree even realize that performance in a (pre-)motor manner.

On-line parameter specification

As pointed out in the introduction, this article deals with the role of perceptual processes in the planning and control of voluntary, goal-directed action. I have considered perceptual processes referring to a broad temporal range: i.e., anticipation based on past perceptions of the effects a given action produced on previous occasions, as well as the impact of the current perceptual environment on action selection. I have discussed evidence that all these processes and informational sources can affect which action we perform to reach a particular goal and perhaps even influence the goals we have. What I did not consider, however, are effects of perceptual information on ongoing behavior. The reason for this is not that such effects do not exist. A particularly convincing demonstration of their existence stems from Prablanc and Pélisson (1990). They had subjects move their hands to a goal position indicated by a light that was sometimes shifted by a few centimeters after the movement had begun. As the shift was carried out during an eye movement of the subjects, they were entirely unaware of it. And yet, their hand moved straight to the new goal location, without any signs of

corrections. Obviously, the movement was adapted to the changed situation in the absence of any conscious awareness of even the fact that a change was taking place (cf. Bridgeman et al. 1979; Goodale et al. 1986).

These and more empirical observations motivated Milner and Goodale 1995 to suggest a neuro-cognitive model of visuo-motor manual action, in which two processing pathways are distinguished. One is an on-line channel that proceeds along the dorsal visuo-motor pathway, segregating in the primary visual cortex and connecting to the motor cortex via relay stations in the posterior parietal cortex. This so-called “action channel” is claimed to provide information about grasp- and reaching-relevant visual information, such as location and size, that directly feeds into systems responsible for hand control. Information processed along this route is not consciously accessible, which fits with the outcomes of reaching studies of the sort discussed above and with the observation that patients suffering from form agnosia are able to properly grasp objects they at the same time are unable to identify (Goodale et al. 1991). The other, off-line channel is assumed to run from primary visual areas straight to the infero-temporal cortex, that is, to areas involved in object recognition. This so-called perceptual channel has access to memory, is consciously accessible, and its main function is restricted to visual perception. Consistent with this claim, an impairment of this channel (as in optic ataxia) has the effect that people may be able to identify an object that they at the same time are unable to grasp (Perenin and Vighetto 1988).

Milner and Goodale’s model has been widely discussed and some, probably too strong assumptions have been challenged (e.g., Bruno 2001; Franz 2001; Jackson 2000). And yet, the general distinction between a memoryless on-line channel that provides ongoing actions with the most up-to-date sensory information and a cognitively penetrated, memory-based off-line channel fares well in the light of the empirical evidence available so far (Rossetti and Pisella 2002). However, it seems questionable whether this distinction is most aptly characterized as dividing action from perception. If the term “action” refers to the performance of movements to reach an intended goal (i.e., to produce an intended effect), it is difficult to see how a processing channel responsible for action control can do without any top-down influence from a memorized goal and without any idea about the expected consequences of the action. It is also difficult to see how a memoryless-action channel can carry out actions that are not driven by stimuli, something humans can easily do. And, indeed, one can doubt whether the essence of intentional action is best described as the “transformation of visual information into spatially calibrated motor outputs”, as Milner and Goodale (1995) characterize the dorsal pathway’s main function.

A more realistic account of the ventral-dorsal separation may take into account the distinction between action plans and their parameters. We have seen evi-

dence that action plans are constructed from past experience, that is, from anticipations of action effects based on previously encountered action-effect contingencies. However, even the best-informed anticipation can only be an approximation of the actual state of affairs, so that action plans are necessarily imprecise. As the actions they generate are commonly as precise as they need to be, we need to assume that action planning underspecifies the intended action and leaves open parameter “slots” to be filled by on-line sensory information (Jeannerod 1984; Schmidt 1975; Turvey 1977). Indeed, this is what observations as those from Prablanc and Pélisson (1990) suggest: When planning a manual reach, people do not pre-specify the target location in absolute coordinates but, rather, pre-specify (i.e., plan offline) the target object, the effector, and the direction of the movement, and leave the on-line specification of the remaining parameters to the environment. Accordingly, a change in an environmentally specified parameter does not change the plan and, thus, need not even be noticed. Milner and Goodale’s dorsal pathway seems to be perfectly equipped to deliver the external evidence needed to specify the open parameters of action plans: it is strictly on-line and thus provides motor systems with the most up-to-date details about movement-related characteristics of goal-relevant objects. In contrast, their ventral pathway has everything needed to guide perception and action planning: it works offline, has access to goals and anticipations, and makes full use of the available knowledge. Accordingly, it seems to be reasonable to characterize the dorsal channel as a *sensorimotor pathway* and the ventral channel as (a part of) a *perception-action system* (Glover 2004; Hommel et al. 2001b). Consistent with this claim, recent studies were able to demonstrate that action planning is affected by cognitive illusions (Glover 2002; Glover and Dixon 2001; Kerzel et al. 2001) and semantic interference (Glover and Dixon 2002), while action execution is not.

Conclusions

The aim of this article was to challenge the still popular view that the relation between perception and action is well captured by the linear, unidirectional processing chains depicted in psychological textbooks. We have discussed evidence that the basic unit of action planning and action control is not a pure output node but, rather, a feature-specific sensorimotor compound that integrates output signals with the input signals they are likely to evoke. Accordingly, planning an action necessarily involves perceptual anticipation and the use of anticipation for planning the action as needed. Sensorimotor units may often be overlearned, but a single action is sufficient to create a new one that is sufficiently stable to affect subsequent action planning. The sensorimotor nature of the elements of action plans renders these plans sensitive to environmental information, in such a way that perceived events can prime feature-

overlapping actions. This has obvious implications for working environments and software ergonomics, but it is also likely to underlie our ability to imitate actions we perceive. In any case, perception and action are not just related, they are two sides of the same coin.

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