

Event files: feature binding in and across perception and action

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The primate brain codes perceived events in a distributed fashion, which raises the question of how the codes referring to the same event are related to each other. Recent findings suggest that they are integrated into 'object files', episodic bindings of object-related information. However, the problem of integrating distributed codes is not restricted to perception but applies to action planning and sensorimotor processing as well. Here I argue that the brain addresses these problems by creating multi-layered networks of bindings – 'event files' – that temporarily link codes of perceptual events, the current task context, and the actions performed therein. These bindings produce systematic but often surprising and counter-intuitive interactions between, and impairments in, perception and action planning.

The primate brain codes the features of perceptual events in a distributed fashion so that, say, the shape, color, and location of a visual object are represented in different feature maps in the visual cortex. This creates binding problems [1], which call for a mechanism that somehow integrates the codes of features belonging to the same event (see Box 1). In this article, I propose that each encounter with a perceived event, such as a briefly presented stimulus, or a to-be-produced event, such as an intentional action, leads to the creation of a transient, episodic 'event file' – a network of bindings that temporarily link codes of the relevant or salient features of the perceptual event, an accompanying action, and the task context. During the lifetime of an event file another encounter with one or more of the bound features causes the automatic retrieval of a larger part of, or even the whole file, a kind of pattern-completion process that might hamper the creation of new event files for feature-overlapping but non-identical events.

Feature integration and the binding problem

Discussions of the binding problem commonly focus on visual perception, where the existence of numerous feature maps can make the need for integration appear most pressing. However, the cortical codes that make up action plans are no less distributed than codes of visual features [2,3], suggesting that planning an action must also involve some sort of feature integration [4]. Moreover, considering that people often carry out more than one task at a time stimuli and responses belonging to the same task

must also be linked to some degree [5]. That is, there is a need to integrate related features in perception, in action planning, and across perception and action. By whatever physiological mechanisms these needs are satisfied, there is evidence that they leave behind what I call event files [6], that is, transient bindings of stimulus and/or action features.

Object files

Kahneman, Treisman, and colleagues [7] were among the first to address the consequences of feature binding in visual perception systematically. By using a PREVIEW TASK (see Glossary), they showed that repeating a visual item facilitates responding to its identity, as one would expect, but that this benefit is mainly restricted to conditions that retain the relation between the identity and the location of that item. They suggest that processing a visual object establishes an 'object file', an episodic trace containing information about the relationship between object

Glossary

Delayed-response task: Task in which subjects prepare a response and hold it prepared until a 'Go' signal appears. Between planning and execution other tasks might be carried out, such as another stimulus–response task [4] (and Figure 1b) or a perceptual judgment [19] (and Figure 1c).

Flanker-compatibility effect: Facilitation/interference induced by the response compatibility of task-irrelevant yet difficult to ignore flanker stimuli surrounding a target stimulus.

Negative priming: Performance deficit obtained if a distracting and to-be-neglected element of a display becomes the target feature in the next trial.

Object-non-specific repetition effect: Effect of repeating a single feature (e.g. shape or color) independent of the repetition or non-repetition of other features. Presumably caused by left-over activation of respective feature code(s).

Object-specific repetition effect: Result pattern in which the effect of repeating a single feature of an object depends on whether or not other features (e.g. location) are repeated as well. Implies that feature codes no longer act independently and, thus, indicates feature binding.

Partial-repetition cost: Result pattern in which repeating some but not all features of an event produces worse performance than repeating all or none of the features. Also shows that (stimulus and/or response) feature codes no longer act independently and, thus, points to feature binding.

Preview task: Task in which a commonly speeded response to a feature of a visual target stimulus is preceded by the presentation of another, task-irrelevant stimulus (or stimuli) that shares none, some, or all features with the target [7] (and Figure 1a).

Prime-probe stimulus-response task: Task in which subjects carry out a previously cued, prepared response (R1) to the mere onset of a stimulus (S1), followed by a speeded forced-choice response (R2) to another stimulus (S2). As R1 is independent from the features of S1 the relations between S1 and S2 features and of R1 and R2 can vary orthogonally [6] (and Figure 1d).

Simon effect: Facilitation (or interference) induced by the spatial compatibility (or incompatibility) between the task-irrelevant location of a stimulus and the correct response.

Stimulus-Onset Asynchrony (SOA): Time elapsed between the onset of one stimulus and onset of another, that is, time available to process one stimulus before processing of the next begins.

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Box 1. Neural mechanisms of feature integration

The integration of distributed feature codes is commonly ascribed to one of three basic mechanisms [41–43] (see Figure 1):

Integration by convergence

This relies on the idea of conjunction detectors, that is, neural units that are selective for the presence of particular feature combinations, such as the red, vertically extended bar in Figure 1. If only one detector per conjunction exists, this mechanism can encode only one event at a time; for example, an attempt to process a green, horizontally extended bar alongside the red, vertically extended bar would activate both shape codes and both color codes, so that all four conjunction detectors would be activated. Proper binding can be achieved by restricting feature encoding to one location at a time [44]. Alternatively, conjunction detectors could be multiplied and monitor only limited areas of the visual field – multiple objects could then be encoded in parallel only if they appear in different locations.

Integration by correlation

A still highly controversial mechanism, this might work by synchronizing the firing patterns of neural units representing features of the same event [41,42]. No separate detector is necessary, synchronicity could increase the impact of the synchronized unit on other processes (e.g. perceptual or response processes). Synchronization in the visual cortex seems to be driven by muscarinic-cholinergic systems [45], which fits with the observation that partial-repetition costs related to shape-location and shape-color binding increase and decrease under the influence of muscarinic-cholinergic agonists and antagonists, respectively [15,40].

Integration by indexing

This might work by enhancing the firing rates of object related neural units [46], which again might support the creation of adaptive, context-sensitive links between them. These links might function as interconnected pointers to object- and action-related feature codes [13,47], a role that has been associated with neural units in prefrontal cortex [43,48,49].

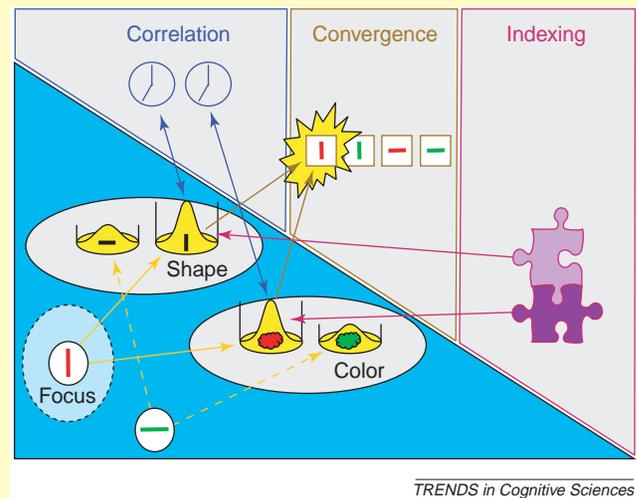


Figure 1. Feature integration by convergence and correlation. The selective encoding of one of two stimuli (the 'focus'), which are defined by two features each: color and shape (orientation). A correlation mechanism codes the conjunction by synchronizing the firing patterns of the feature-specific neural units so that, in this case, the units coding 'vertical' and 'red' will fire in synchrony. A convergence mechanism codes for feature conjunctions, so that activating the codes 'vertical' and 'red' will propagate to a vertical-red conjunction detector. An indexing mechanism establishes interlinked pointers to the respective feature codes, that is, 'vertical' and 'red'.

Given the numerous hints to the presence of all three mechanisms in the primate brain [43,50,51] it is likely that they serve different and presumably complementary functions. Indeed, creating a conjunction detector makes sense for processing highly probable, evolutionary important feature conjunctions, whereas integration by correlation or indexing seems to be the optimal way to code arbitrary, frequently changing feature relations. Also, correlation could be the neural language in which feature codes and their pointers communicate.

features, possibly enriched by object-related knowledge from long-term memory, and addressed via location codes [7,8]. When reviewing an object with most of its features retained, an update of the old object file will do, whereas an entirely new object requires the time-consuming construction of a new file.

Even though the basic finding of a relative benefit for the repetition of identity–location conjunctions has been frequently replicated (e.g. [9]), the original object file account is in need of modification with regard to three aspects. First, whereas Kahneman *et al.* found hardly any evidence for OBJECT-NONSPECIFIC REPETITION EFFECTS, other studies were more successful in this respect [10,11]. Very probably, variations in STIMULUS-ONSET ASYNCHRONY (SOA) are responsible for these contrasting findings: object-nonspecific effects dominate at short SOAs – that is, when prime and probe stimuli appear in brief succession – and give way to OBJECT-SPECIFIC REPETITION EFFECTS as SOA increases [12]. Object-nonspecific feature priming not only precedes objects-specific effects (thus reversing the scenario Kahneman *et al.* envisioned), it also seems to be involved in producing them. This is suggested by the finding that nonspecific and specific effects are correlated (Colzato, Warrens and Hommel, unpublished) and

similarly affected by manipulating the task relevance of particular features [6,12].

Second, Kahneman *et al.* assumed that object files are exclusively addressed by location, that is, the feature content of a file would only be available if a probe object can be spatially related to a prime object. However, infants and children have been shown to use (changes in) nonspatial features to individuate objects and spatio-temporally extended events, which suggests that object files can be addressed via any feature they contain [13]. Moreover, the addressing-by-location assumption implies a stronger impact of location changes on object-specific effects than empirical findings confirm; for instance, bindings between nonspatial features (e.g. shape and color) can affect performance even if the object location changes [6,12]. Thus, what is addressed does not seem to be a complete binding of all features of an object, not even of all attended features; instead, feature conjunctions commonly seem to be represented by several separate, binary bindings, a loose network of clusters rather than one master file [6,12]. The likelihood that a given feature becomes part of one or more bindings seems to be high (i) if it is signaling some response in the entire task context (not necessarily at the time the binding takes place) [6,14],

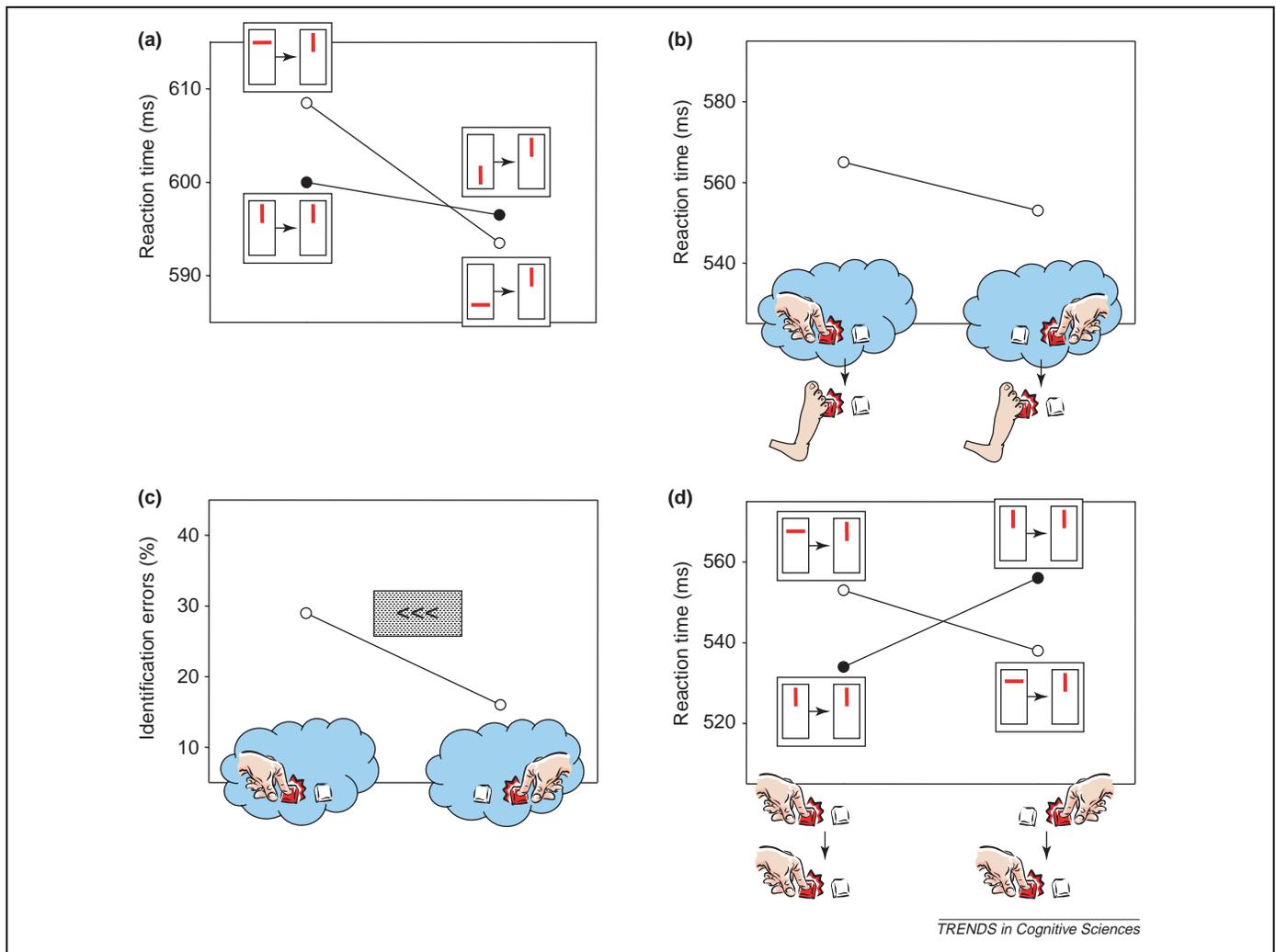


Figure 1. Representative data patterns from studies showing effects of feature binding in perception and action planning (all shown interactions are reliable). **(a)** repeating or changing shape *and* location from one part of a trial to the next (a preview task) produces better performance than changing only one feature and repeating the other (ignoring the overall benefit for location changes, known as ‘inhibition of return’). This suggests shape–location binding in visual perception. (Data redrawn from [6]); **(b)** preparing and holding prepared a manual action with the left or right hand (a delayed-response task) delays the planning of a spatially corresponding foot response, suggesting effector–location binding in action planning. (Data redrawn from [4]); **(c)** preparing and holding prepared a left or right manual action (a delayed-response task) impairs the discrimination of a spatially compatible arrow head, suggesting an effect of action–location binding in action planning on perception. (Data redrawn from [19]); **(d)** repeating or changing shape *and* response from one part of a trial to the next (a prime-probe stimulus–response task) produces better performance than changing only one and repeating the other, which suggests shape–response binding. (Data redrawn from [6].)

or (ii) if it varies on a dimension that is somehow relevant for the task, such as location in a task using spatially defined responses; and it might be non-zero if it is task-irrelevant but perceptually salient [12].

Third, object-specific effects do not seem so much to reflect a benefit for cases in which an object is repeated but, rather, processing costs incurred by repeating some but not other features of a just integrated object. As Figure 1a shows, repeating two given features (shape and location in that example) produces good performance that however is no better than conditions in which no feature repeats, a pattern that has been demonstrated for other conjunctions as well [6,12,15] and that we will meet again below. Apparently, activating a wrong file impairs performance more than is helped by having an appropriate object file available. This suggests that feature binding produces PARTIAL-REPETITION COSTS rather than object-specific repetition benefits [12]. It also suggests that updating an object file (i.e. changing one or more

elements of an existing file) is a time-costly and error-prone process.

Taken together, the available evidence suggests that encountering a perceptual object primes the corresponding codes to a degree that is weighted by task relevance (and, perhaps, salience) (see Figure 2). Sufficiently primed features can enter several, often binary bindings that survive for 4 s or longer [12]. Reviewing one or more of the bound features retrieves the corresponding event file(s), which hampers performance if the codes they contain are not entirely consistent with the present perceptual event. Reviewing an event will re-activate the previously created event file if (and to the degree that) it shares features with the event represented thereby. This hampers performance if the match is only partial, that is, if some but not all features are shared. In the example in Figure 2, if the next stimulus were a red, horizontal bar in the same top location, the event file shown would be retrieved, which would spread activation to the wrong, vertical shape code

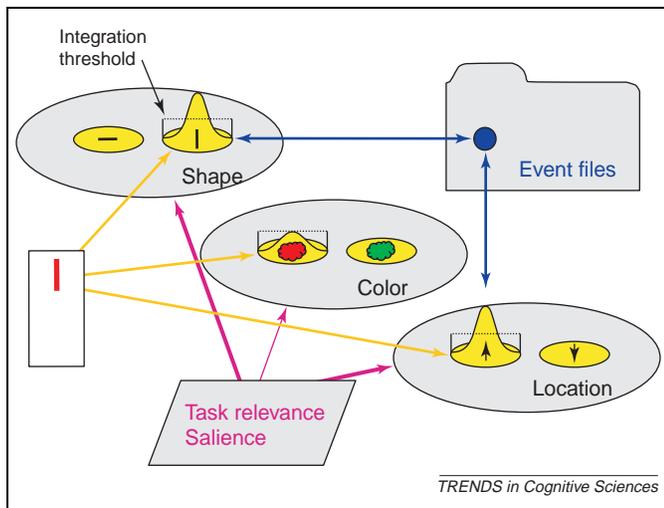


Figure 2. A model of feature integration. The example shows the processing of a single visual stimulus defined by shape, color and location. Shape is assumed to be directly task relevant (e.g. because it specifies a response) and location is assumed to be indirectly task relevant (e.g. because responses are defined by location). The features are coded on different, dimensionally organized feature maps. Task-relevant dimensions are primed, so that features coded thereon are activated more highly (very salient, task-irrelevant features might also get activated to some degree). Adjustable integration thresholds define the degree of activation necessary to become considered for integration. If codes pass the threshold they become 'bound' into an event file, that is, they are assigned a pointer, index, or other short-term association linking them with one or more other feature codes (including codes of response features, see Box 2). In this way, episodic instances or 'tokens' are represented as context-dependent links between stimulus representations, or 'types' – links that may or may not include reference to place and time.

and delay identification. If the two shapes were mapped onto different responses, this activation might even propagate to the incorrect response and create a response conflict.

Action files

Considering the distributed, effect- or goal-based representation of actions (see Box 2), it is likely that action planning faces similar binding problems as involved in processing an object and it makes sense to assume that it uses similar mechanisms to solve them [2–4]. If so, planning a particular action should involve binding the features of that action to a plan or, in keeping with Kahneman *et al.*'s terminology, to an 'action file' [4,16]. Once a feature is bound to plan A, it should become more difficult to plan another action B that includes the same feature as long as plan A has not been performed (and the respective action file is maintained). Indeed, planning a movement with the left (or right) hand and maintaining that plan (a DELAYED-RESPONSE TASK) impairs the planning of another movement with the same hand or leg until the first plan is carried out [4] (see Figure 1b). Similarly, planning a verbal utterance after having prepared another, now signaled to be invalid utterance is easier if the former does not share (phonetic) features with the latter than if the two partially overlap [17]. Likewise, repeating an utterance is more difficult if the combination between phonemes and stress level frequently changes [18]. Thus, planning an action indeed seems to bind codes representing the features of that action. As a consequence, these codes are less available for other planning activities until the original plan is executed.

Box 2. The representation of action

The notion of action planning as a binding process that integrates codes of the features that the intended action ought to have, emphasizes and exploits the commonality between perceiving and producing events, that is, between perception and action planning. Several lines of research motivate this emphasis.

Ideomotor approaches to action control have seen a renaissance in recent years [3,52]. They claim that control of human action emerges from self-perception: performing a movement leaves behind a bidirectional association between the motor pattern it was generated by and the sensory effects it produces (movement ↔ effect). Once acquired, these associations can be used 'backwards' to retrieve a movement by 'anticipating' its effects (effect → movement), that is, by selecting actions with respect to their perceptual consequences [53,54]. The tight relationship between perception and action that these anticipatory control mechanisms imply could explain numerous phenomena in stimulus-response compatibility, imitation, motor imagery, and dual-task interference (for an overview, see [16]).

The discovery of **mirror neurons** provides further support for a functional and neuroanatomical overlap of perceptual and action-related codes (for an overview, see [55]). Single-cell recordings in the inferior premotor cortex (PMC) of the macaque monkey and brain activity in the human homologue of PMC have been demonstrated to code both the production and the perception of goal-directed action, such as grasping an object. It has been argued that the existence of such a mirror system facilitates the acquisition of action and language, and could provide the basis for empathy and mind reading [56].

Recent findings suggest important contributions of the human PMC to the anticipation of perceptual events (for an overview, see [57]). This might indicate a dual function of PMC in generating motor output and regulating action-related perceptual and attentional functions. That is, actions and their expected consequences might be integrated in a 'habitual pragmatic body map' [57] located in PMC.

Event files

The observation of binding-type effects in object perception and action planning suggests that feature integration is a general phenomenon and that linking the codes belonging to the same event is a universal way to deal with processing problems arising from our brain's preference for distributed representation. If so, one would expect that features are not only locally integrated but bound across representational domains as well. Indeed, there is strong evidence that binding in perception affects action planning, and vice versa, and that stimulus features can become bound to action features.

Binding in action affects perception, and vice versa

The impact of action planning on perceptual binding is obvious from the demonstration that planning a manual left or right movement and maintaining that plan (a delayed-response task) impairs the perception and even the detection of spatially corresponding, briefly presented and masked stimuli (e.g. arrows) [19,20] (see Figure 1c). Thus, binding a particular spatial code to an action plan impairs both planning another action and integrating a perceptual event requiring that code, suggesting that event representation in perception and action makes use of the same type of codes [16], at least to some degree. Indeed, binding a code to a perceptual event representation can also affect action planning: holding a left- or right- side object in working memory slows down reaction time for actions carried out at the same side [21].

Binding a code to an action plan can also exert qualitative effects on perception, and vice versa – a phenomenon that is observed if perceptual and action events vary on a finer-grained dimension than left versus right. For instance, when people perceive cursor movements of different amplitudes while performing cursor-unrelated hand movements with different amplitudes, they tend to increase the contrast between seen and performed movements: with regard to action, large-amplitude stimuli induce a decrease and small-amplitude stimuli an increase of the performed amplitude and, with regard to perception, performing a large- or small-amplitude movement induces an under- and overestimation of the perceived stimulus amplitude, respectively [22,23]. Comparable effects are obtained when subjects judge the weight of a box lifted by an actor while lifting a light or heavy box themselves [24]: the observed box is judged to be heavier when subjects lift a light box and judged to be lighter when they lift the heavy box.

Contrast effects of that sort (see also [25,26]) are consistent with the claim that action parameters are coded by populations of broadly tuned neurons [27,28]. For instance, neurons coding the direction of a reach show the greatest activity at their preferred direction but also contribute to coding neighboring directions [26]. As a consequence, binding such a cell to an action plan and thereby ‘occupying’ the respective code would not only make it more difficult to access for other representational purposes but also exaggerate the difference between the direction involved in the plan and those directions that are not (cf. [22,24]). Assuming that population coding is a general principle in the primate cortex [28] and considering that codes are shared by event coding in perception and action [16], binding in action planning can thus account for contrast effects in perception and vice versa.

Binding across perception and action

Interactions between perception and action planning show that codes are shared between these two domains. Evidence for binding across domain borders comes from studies where the repetition or alternation of stimulus features and the responses varied independently [6,12,29] – a PRIME-PROBE STIMULUS-RESPONSE TASK. Figure 1d shows a typical outcome: alternating both a stimulus feature (shape in this example) and the response yields performance that is as good as repeating both. That is, as we have seen for repetitions of multiple stimulus features (Figure 1a), performance is impaired on partial repetitions. Apparently, then, reviewing a stimulus feature tends to activate the response it previously accompanied, and vice versa, which creates response or stimulus competition if the activated former companion is now incorrect and unwanted. As in the creation of object files, not all stimulus features get bound with the response but only those that are directly or indirectly task-relevant or salient (Figure 2).

Bindings between stimulus features and the response have the theoretically very interesting property of mimicking several effects that are often attributed to other, commonly inhibitory and/or strategic processes. For instance, there is evidence that at least substantial

portions of NEGATIVE PRIMING [30], ‘automatic route suppression’ in the FLANKER-COMPATIBILITY EFFECT [31] and the SIMON EFFECT [32] are actually produced by the impact of event files formed in the previous trial (see [33,34,35] for feature-integration accounts of the respective effects). Stimulus–response bindings are also likely to be responsible for an otherwise counterintuitive observation in studies on repetition effects: trials in which the response but not the (visual or auditory) stimulus is repeated often yield *worse* performance than trials in which neither stimulus nor response are repeated [36,37]. Obviously, these two conditions represent the two right-most data points in Figure 1d and the seemingly odd finding (which until now has motivated numerous post-hoc explanations) is nicely predicted by the present account. Along these lines, substantial portions of the so-called ‘residual’ task-shifting costs [38] have been demonstrated to go back to bindings between particular stimuli with the task set under which they were previously encountered [39]. That is, carrying out a task on a stimulus leaves a trace linking this stimulus to the current task set, so that encountering the stimulus again will tend to retrieve that set – which is especially disruptive if another task set has to be chosen.

Conclusions

Feature binding seems to be a general process subserving the integration of distributed feature codes in object perception and action planning. Binding in perception can impair binding in action planning, or vice versa, by occupying codes of overlapping features, which can yield a delay of creating a new binding and/or modify the content of the eventual plan or percept. What is more, binding takes place across domains, linking relevant or salient features of the stimulus to the response it is accompanied by and the task set it is processed in. Hence, there are reasons to believe that object and action files belong to the more general category of event files [6].

Event files are created by a single co-occurrence of the bound features and they can affect other processes instantaneously. However, this does not mean that they consist of a unitary structure or that their creation is a unitary process. What speaks against the former is that interactions between feature-repetition effects are often only binary – that is, they do not enter higher-order interactions – and that their relations are not transitive – that is, a feature A often interacts with both feature B and feature C in the absence of any interaction between B and C [6]. What speaks against an unitary integration process is the observation that some drugs modulate effects indicative of bindings between visual stimulus features in a systematic fashion without having any impact on stimulus–response bindings [16,40] (Box 1). Thus, events are represented by a network of rather loosely linked codes rather than an orderly master file, at least after a single encounter [6].

The issue of feature integration is well established in object perception but rather uncommon if it comes to action planning or sensorimotor processing. I have discussed several theoretical reasons why in these areas a feature-integration perspective seems appropriate, too, and several studies with often rather counter-intuitive

Box 3. Questions for future research

- How is an event defined? This question is notoriously difficult with regard to perceptual objects and it is even more difficult regarding events. When and under which (exogenous and endogenous) circumstances will a percept and an action plan be integrated into the same event file, and when into separate files?
- Which codes can be integrated, and with what? There is evidence for binding within visual, auditory, and action-related codes, as well as for cross-domain, visuo-manual bindings. But what about audio-visual and manual-verbal bindings, or the integration of affective codes [3]?
- How is binding related to learning? According to Hebb's learning rule ('codes that fire together wire together') binding might be the first step towards creating an enduring memory trace. Does this imply that binding decreases as learning progresses or, to the contrary, that memory traces facilitate and increase binding?

outcomes showing that the perspective is promising and empirically fruitful. Clearly, numerous questions remain to be answered (see Box 3) but attempting to do so is likely to increase our insights into the interplay of perception and action, and the way our brain deals with distributed representations.

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