

Note

Feature binding and affect: Emotional modulation of visuo-motor integration

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Abstract

The primate cortex represents the external world in a distributed fashion, which calls for a mechanism that integrates and binds the features of a perceived or processed event. Animal and patients studies provide evidence that feature binding in the visual cortex is driven by the muscarinic–cholinergic system, whereas visuo-motor integration may be under dopaminergic control. Consistent with this scenario, we present indication that the binding of visual and action features is modulated by emotions through the probable stimulation of the dopaminergic system. Interestingly, the impact of emotions on binding was restricted to tasks in which shape was task-relevant, suggesting that extracting affective information is not automatic but requires attention to shape.

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Representation of objects and actions are distributed throughout the whole brain and each single event activates large numbers of feature-related codes in different representational maps. For example, perceiving a black cat sleeping on the couch involves the coding of the black color in a color map, of the cat's silhouette in a shape map, of its position on in a location map, and so forth (for overviews, see Cowey, 1985; DeYoe & Van Essen, 1988). Distributed coding introduces the so-called binding problem and raises the question of how brains integrate the information belonging to the same event without mixing them up with features from other, concurrently processed events. As suggested by Kahneman, Treisman, and Gibbs (1992), people may create temporary folders or *object files* that contain all the perceptual information about an object. However, binding problems are not restricted to perception but also occur in action planning, which involves numerous neural maps that code the features of the intended action (Stoet & Hommel, 1999), and sensorimotor coordination (Hommel, 1998). This suggests that people create all sorts of *event files*, that is, episodic memory traces containing perceptual as well as action-related information (Hommel, 1998, 2004; Logan, 1988). At the neural level,

a plausible medium to communicate belongingness to the same event is the temporal synchronization of the firing patterns of all the cell populations that represent the different features of a given object or action (Engel & Singer, 2001).

1. Affect and neuromodulation of feature integration

Preliminary evidence suggests that at least two neurotransmitter systems are involved in feature integration and the creation of temporal coherence between cell populations: the muscarinic–cholinergic system, which seems to be related to perceptual binding (Rodriguez, Kallenbach, Singer, & Munk, 2004), and the dopaminergic system, which seems to play a role in the integration of action-related information (Schnitzler & Gross, 2005).

Given this preliminary evidence with respect to neural coherence, it is possible to speculate that (local) visual–visual binding (i.e., integration across different feature maps in the occipital lobe) is driven by the muscarinic–cholinergic system, whereas the integration of stimulus features and actions (which implies more global, interarea communication between distant brain areas) is under dopaminergic control. Indeed, recent drug studies on visuo-motor feature integration (Colzato, Erasmus, & Hommel, 2004; Colzato, Fagioli, Erasmus, & Hommel, 2005)

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revealed that the impact of visual–visual bindings, but not visuo-motor bindings, on behavior can be systematically increased and decreased by administering muscarinic–cholinergic agonists and antagonists, respectively. Comparable studies targeting the dopaminergic system are not available, but patient studies support Schnitzler and Gross' claim: in Parkinson's disease (Brown, 2003) the dopaminergic neurons of the substantia nigra pars compacta (SNc) degenerate, which leads to increased neuronal firing and enhanced oscillatory and synchronized activity of the subthalamic nucleus (STN), and results in excessive inhibition of the thalamocortical drive. Global, long-range oscillatory synchronization constitutes a fundamental mechanism for implementing coordinated communication between spatially distributed local networks in the brain and in Parkinson's disease, because of the dopamine depletion, this kind of synchronization is abnormal.

Interestingly, the functioning of the dopaminergic system seems to be modulated by affective states. Growing evidence shows that positive affect has an influence on a broad range of cognitive processes, generally leading to higher cognitive flexibility (Greene & Noice, 1988; Isen & Daubman, 1984; Isen, Daubman, & Nowicki, 1987; Isen, Niedenthal, & Cantor, 1992; Kuhl & Kazèn, 1999; Phillips, Bull, Adams, & Fraser, 2002). As demonstrated in a recent fMRI study (Dolcos & McCarthy, 2006), impaired performance in the presence of emotional distracters is associated with both enhanced activity in the brain regions responsible for emotional processing and disrupted activity in the brain regions responsible for active maintenance of goal-relevant information in working memory. Ashby et al. (Ashby, Isen, & Turken, 1999; Ashby, Valentin, & Turken, 2002) have suggested that the cognitive impact of positive affect is modulated by increased brain dopamine levels in prefrontal areas, as a result of which the ability to overcome dominant responses is enhanced and cognitive flexibility is increased. Further arguments for a link between dopaminergic activity and cognitive control come from Cohen et al. (Braver & Cohen, 2000; Cohen, Braver, & Brown, 2002). These authors propose that phasic increases of dopamine in prefrontal cortex (PFC), elicited by reward-predicting stimuli, serve as a gating signal, thereby triggering the updating of working memory and facilitating a switch of cognitive set. When unanticipated reward is administered it stimulates the ventral tegmental area (VTA) cells that project to nucleus accumbens, which is well known to play a central role in the reward system. Positive and negative feedback can, thus, have opposite effects on dopaminergic activity. Negative feedback is supposed to decrease dopaminergic activity (Holroyd & Coles, 2002; Mark, Blander, & Hoebel, 1991; Suri, 2002), while positive feedback has been shown to increase dopamine levels (Robbins & Everitt, 1995). Importantly for our study, emotionally arousing pictures with positive or negative valence seem to affect the dopaminergic system the same way as positive and negative feedback does. For instance, Dreisbach and Goschke (2004) observed increased cognitive flexibility (better performance in task switching) when subjects were presented with pictures of positive valence, an effect that is also observed in subjects with chronically heightened dopamine levels (Dreisbach et al., 2005).

2. Purpose of study

Our study was motivated by the idea that the integration of visual features and actions (or action features) might be driven or at least modulated by the dopaminergic system. If this would be the case, and if the activity of the dopaminergic system can be systematically affected by the presentation of pictures with a positive and negative valence (Dreisbach & Goschke, 2004), we should be able to demonstrate that behavioral measures of visuo-motor binding are systematically affected by emotionally arousing pictures. In particular, we would expect pictures of positive valence to increase binding effects across perception and action, and negative pictures to weaken such effects, whereas visual–visual binding should not be impacted by valence.

A second aim of our study was to determine, if picture-induced affect has an impact at all, under which circumstances such affect can impact binding. Previous research (Hommel, 1998, *in press*) showed that the strength of binding effect is dependent on the task relevance of the respective feature dimension: stimulus features from task-relevant, and therefore attended dimensions are bound to the response more strongly than task-irrelevant stimulus features, suggesting that at least some aspects of the creation and/or the retrieval of bindings are under attentional control. One might suspect that the identification of positive and negative valence of pictures requires the processing of shape information, while location and color information is less relevant. For example, when facing the picture of a gun, only by processing its shape we can tell that this is a dangerous object. In contrast, whether the picture is colored or black-and-white, or whether it is presented at one or another location on a screen is of only minor, if any, relevance for determining its affective implications. Accordingly, it may be that the valence of the pictures can affect the integration of shape information more, or only, if shape information is sufficiently task-relevant. To test this possibility we carried out three experiments, which only differed with respect to the relevant stimulus dimension: shape, location, or color.

As behavioral marker for feature-integration processes we adopted a variation of the task developed by Hommel (1998), which taps into both visual–visual and visuo-motor binding and allows varying the task relevance of stimulus features. In this task, each trial comprises of two stimuli and two responses, and each stimulus feature (be it task-relevant or not) and the response can repeat or alternate (see Fig. 1). The typical findings are interactions involving the stimulus features and the response (for an overview, see Hommel, 2004), and they all follow the same pattern: Performance is impaired in partial-repetition trials, that is, if one stimulus feature (or the response) is repeated, while the other feature is not (e.g., performance is worse if the shape is repeated but the response changes, or if the response repeats but the shape does not, than if shape and response are both repeated or both alternated). This demonstrates that the simple co-occurrence of a feature–feature or feature–response conjunction is sufficient to create a temporary spontaneous binding of the respective codes, a kind of “event file” (Hommel, 1998, 2004; Hommel & Colzato, 2004). Repeating one feature reactivates not only the corresponding code but also the associated

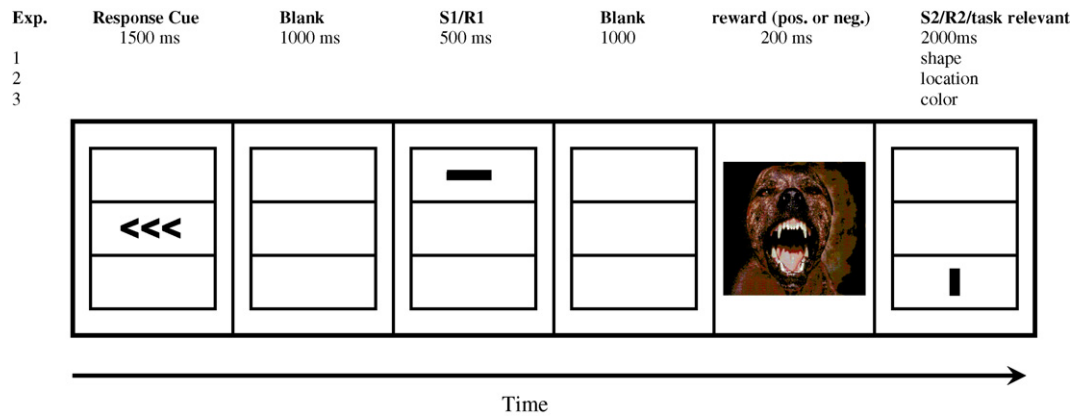


Fig. 1. Sequence of events. A response cue signaled a left or right key press (R1) that was to be delayed until presentation of S1, a red or green (only in experiment 3), vertical or horizontal line in a top or bottom box. If R1 was correct subjects received, as positive or negative reward, a negative or positive emotionally arousing picture. S2 appeared 1 s later—another red or green (only in experiment 3), vertical or horizontal line in the top or bottom box. S2 shape (experiment 1), location (experiment 2), color (experiment 3) signaled R2, also a speeded left or right key press. R2 speed and accuracy were analyzed as function of the repetition vs. alternation of stimulus shape, color, and location, and of the response. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

“fellow code”, which creates a mismatch if the feature coded by that code was changed. This mismatch-induced conflict induces a time-consuming update or re-binding process, which impairs performance in partial-repetition trials.

Crucially for our purposes is that, first, these partial-repetition costs can be taken to indicate feature–feature (visual–visual) and feature–response (visuo-motor) binding. Second, with the task adapted from Hommel (1998) we can easily vary the dimension to which the subjects react to in S2 (R2), to see whether this affects the impact of the pictures on performance and binding.

In sum, we expected that presenting affectively positive and negative pictures would induce corresponding affective states that (presumably via the dopaminergic system) would increase or decrease the integration of visual stimulus features and the response. If so, the affective manipulation should increase and decrease partial-repetition costs, respectively. Across three experiments we varied the task-relevant feature: shape (in experiment 1), location (in experiment 2) and color (in experiment 3). If pictures would be processed and impact binding only if shape is task-relevant, we would expect affect to modulate the binding of the task-relevant stimulus feature and the response in experiment 1 but not in the other experiments.

3. Methods and subjects

Twenty-three, 23, and 22 young healthy adults served as subjects in experiments 1–3, respectively. Subjects performed a task modeled after Hommel (1998) (see Fig. 1). In experiment 1 they faced three green, vertically arranged boxes in the middle of a monitor and carried out two responses per trial. R1 was a delayed simple reaction with the left or right key, as indicated by a 100%-valid response cue (three left- or right-pointing arrows in the middle box) that preceded the trigger stimulus S1 by 3000 ms. S1 varied randomly in shape (a thin vertical or horizontal line) and location (top or bottom box). R1 was to be carried out as soon as S1 appeared, independent of its shape, color, or location; i.e., subjects were encouraged to respond to the mere onset of S1. If R1 was correct subjects were presented with a positive or negative emotionally arousing picture for 200 ms. Note that the affective tone of the picture was not correlated with, and did not depend on the accuracy of the response; i.e., the probability to receive a positive or negative picture after a correct response was 50:50. The 32 pictures (16 positive and 16 negative valence) were chosen from the Inter-

national Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005), a set of standardized emotional stimuli for experimental investigations of emotion and attention.

R2 was a binary-choice reaction to the shape of S2 (vertical or horizontal orientation), which also appeared in the top or bottom box, 1000 ms after S1 onset. Responses to S1 and to S2 were made by pressing the left or right shift-key of the computer keyboard with the corresponding index finger. If the responses were incorrect auditory feedback was presented.

The procedure of experiment 2 was the same as in experiment 1, with the following exceptions. Subjects had to react not to the shape but to the location of S2 (top or bottom). Experiment 3¹ followed the same line of experiments 1 and 2, apart from these exceptions: S1 and S2 varied not only in shape (vertical versus horizontal) and in location (top versus bottom) but also in color (green versus red); R2 was a binary-choice reaction to the color (green versus red) of S2; and the vertically arranged boxes were grey.

4. Results

After excluding trials with missing (>1500 ms) or anticipatory responses (<200 ms), mean reaction times (RTs) and proportions of errors for R2 were analyzed by ANOVAs. Data from experiments 1 and 2 were analyzed using a four-way design, as a function of emotional valence of the pictures (negative versus positive) and the repetition versus alternation of response (R → R2), stimulus shape and location (S1 → S2). Data from experiment 3 were analyzed using a five-way design, as a function of valence and the repetition versus alternation of response, stimulus shape, location, and color. Table 1 presents the group means for all conditions and experiments.

4.1. Experiment 1 (shape relevant)

This experiment replicated earlier findings (Hommel, 1998; Hommel & Colzato, 2004). RTs revealed two significant interactions indicative of binding effects, one between shape and

¹ For reason unrelated to the present study we varied three feature dimension. Previous studies (Colzato, Raffone, & Hommel, 2006) did not provide evidence that the numbers of features varied has an effect on binding effects, so that our conclusion will not be affected by this manipulation.

Table 1

Means of mean reaction times for responses to stimulus 2 (RT; in ms) and percentages of errors on R2 (PE), as a function of experiments, emotional valence of the pictures, the match between response 1 and response 2, and the feature match between stimulus 1 and stimulus 2

Match	Experiment 1 (Shape relevant)								Experiment 2 (Location relevant)							
	Positive valence				Negative valence				Positive valence				Negative valence			
	Repeated ^a		Alternated ^a		Repeated ^a		Alternated ^a		Repeated ^a		Alternated ^a		Repeated ^a		Alternated ^a	
	RT	PE	RT	PE	RT	PE	RT	PE	RT	PE	RT	PE	RT	PE	RT	PE
Neither	519	15.0	505	6.4	521	13.4	489	7.8	484	14.7	461	6.5	476	15.2	466	7.8
S (shape)	518	13.8	528	12.3	522	12.1	520	13.4	485	13.8	456	8.0	484	11.0	466	8.9
L (location)	519	12.5	513	9.3	540	12.5	504	7.2	476	7.6	484	15.2	476	10.7	491	14.7
SL	513	10.6	535	11.2	505	10.6	529	14.0	463	9.4	486	14.3	459	9.0	490	15.9

Match	Experiment 3 (Color relevant)							
	Positive valence				Negative valence			
	Repeated ^a		Alternated ^a		Repeated ^a		Alternated ^a	
	RT	PE	RT	PE	RT	PE	RT	PE
Neither	530	19.9	486	10.2	527	19.6	480	11.6
S (shape)	528	18.7	491	6.2	533	17.6	476	7.9
C (color)	507	11.9	514	9.4	504	10.8	509	12.5
L (location)	522	20.2	498	7.7	526	19.2	486	8.5
SC	496	13.1	513	15.6	502	13.3	513	14.2
SL	529	15.6	488	6.5	522	17.6	503	8.8
CL	481	9.4	501	14.8	494	11.9	508	17.6
SCL	490	9.1	508	17.6	474	12.5	513	17.9

^a Response.

location, $F(1,22)=4.81$, $p<.04$, and one between shape and response, $F(1,22)=19.24$, $p<.001$.

The first interaction was due to that repeating shape and location (521 ms) or neither (509 ms) yielded better performance than repeating shape and alternating location (522 ms) or vice versa (520 ms), at least if one corrects for the (unreliable) 7-ms advantage for shape alternations. Consistent with previous research, the mere co-activation of a shape code and a location code was apparently sufficient to integrate the two. Repeating shape or location induced the retrieval of this binding, which created code conflict if the previous fellow feature alternated.

The second interaction followed the same pattern by showing that repeating shape and response or neither yielded better performance than the repetition of one but not the other (see Fig. 2). As demonstrated earlier, pairing a particular stimulus with a response creates a binding between their codes, which induces code conflict in case of a partial repetition. Consistent with Hommel (1998), only the task-relevant stimulus feature interacted with the response, whereas the interaction between location repetition and response repetition was not reliable, $F(1,22)=2.87$, $p<.11$. Most importantly, the interaction between shape and response was modified by the emotional valence of the pictures, $F(1,22)=6.52$, $p<.02$, while the interactions of valence with location and response, with shape and location, and with shape, location, and response were all far from significance ($p>.92$, $p>.17$, and $p>.20$, respectively).

Finally, there was an interaction between response repetition and valence, $F(1,22)=8.74$, $p<.01$. It was due to that response

repetitions yielded faster RTs than alternations after positive pictures (517 ms versus 522 ms) but slower RTs after negative pictures (520 ms versus 511 ms). Given that this effect did not replicate in experiments 2 and 3, it needs to be interpreted with caution.

The errors followed a similar pattern as the RTs. There was a main effect of shape, $F(1,22)=4.64$, $p<.05$, and response repetition, $F(1,22)=5.57$, $p<.03$, and a significant interaction between these variables, $F(1,22)=13.27$, $p<.002$. The latter indicated fewer errors in conditions where shape and response were both repeated or both alternated than in the partial-overlap conditions.

4.2. Experiment 2 (location relevant)

Experiment 2 replicated the first experiment for the most part. We obtained significant two-way interactions between shape and location, $F(1,22)=4.92$, $p<.04$, between location and response, $F(1,22)=17.42$, $p<.001$, while shape and response did not interact, $p>.28$. As in experiment 1, and considering the (unreliable) 6-ms advantage for location alternations, repeating shape and location (475 ms) or neither (472 ms) yielded better performance than repeating shape and alternating location (473 ms) or vice versa (482 ms). Similarly, repeating location and response or neither produced better performance than repeating one but not the other (see Fig. 2). Hence, location played the same role that shape had played in experiment 1. The only remaining effect was a three-way interaction between

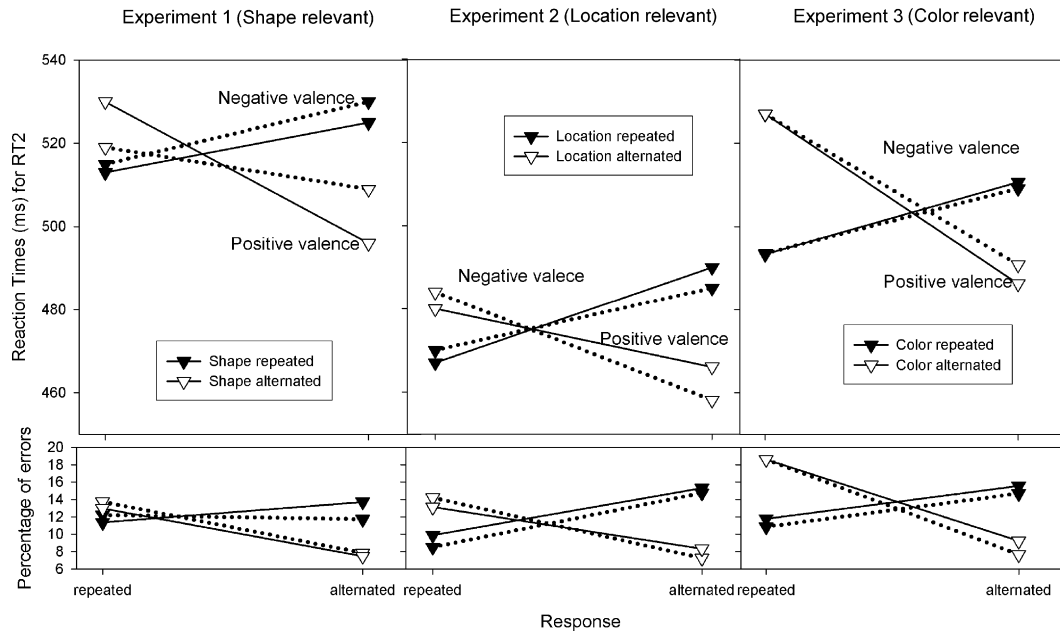


Fig. 2. Mean reaction times and error percentages for RT2 for experiments 1–3, as a function of reward (positive = straight line and negative = dotted line), repetition vs. alternation of stimulus task-relevant feature and response. Typical binding effects are indicated by patterns showing worse performance for filled triangle on the left and unfilled triangle on the right (one stimulus feature is repeated while the response alternates, or vice versa). Only in experiment 1, where the task-relevant feature was shape, reward affected the sensori-motor binding: positive reward increased binding effect between shape and response.

shape, location, and response, $F(1,22) = 11.56$, $p < .003$. It was due to that the location-by-response interaction was more pronounced if shape was repeated, which indicates that even the irrelevant shape was integrated to some degree. Most importantly, there was no evidence of any impact of valence, especially the three-way interactions involving valence and the four-way interaction were all far from significance, p 's $> .46$. The error results mirrored RTs, yielding interactions between location and response, $F(1,22) = 30.61$, $p < .001$, and between shape, location, and response, $F(1,22) = 5.66$, $p < .03$.

4.3. Experiment 3 (color relevant)

RT results showed significant interactions between location and color, $F(1,21) = 5.62$, $p < .03$, color and response, $F(1,21) = 60.06$, $p < .001$, and location and response, $F(1,21) = 8.28$, $p < .009$. Repeating color and location (496 ms) or neither (507 ms) yielded better performance than repeating color and alternating location (507 ms) or vice versa (509 ms), at least if one corrects for the (unreliable) 6-ms advantage for color repetitions. Similarly, repeating color and response or neither produced better performance than repeating one but not the other (see Fig. 2). Here, color played the same role that shape had played in experiment 1. However, the interaction of location and response indicates that even though color was the only nominally relevant stimulus feature, location was ignored altogether. As in experiment 2, valence had no impact, the three-way or higher-order interactions involving valence all missed significance, p 's $> .14$. The error analysis yielded only an interaction between color and response, $F(1,21) = 49.90$, $p < .001$, which followed the same pattern as the RT effect.

5. Discussion

All three experiments were consistent with previous findings (Hommel, 1998) in indicating that the task-relevant stimulus feature is more strongly bound to the response than task-irrelevant stimulus features. This suggests that either the creation or the retrieval (or both) are under attentional control (Colzato et al., 2006). As anticipated, affect modulated visuo-motor binding only when shape was the task-relevant feature. Taken together our results suggest two conclusions.

First, our findings are in line with the following links: (a) between affect and higher cognitive flexibility (Dreisbach & Goschke, 2004; Greene & Noice, 1988; Isen & Daubman, 1984; Isen et al., 1987, 1992; Kuhl & Kazén, 1999; Phillips et al., 2002); (b) between affective action consequences and the dopaminergic system (Ashby et al., 2002; Holroyd & Coles, 2002; Mark et al., 1991; Robbins & Everitt, 1995; Suri, 2002); (c) between the dopaminergic system and neural synchronization (Schnitzler & Gross, 2005); and (d) between synchronization and feature integration (Abeles, 1991; Engel & Singer, 2001). In particular, the outcome of our study demonstrates that positive and negative consequences of a response modulate the binding of that response to the task-relevant visual feature, while sparing bindings between visual features. The tight connection between visuo-motor integration and action outcomes fits with a recent observation of Hommel (2005). In that study, the first, prepared response (R1) was triggered by a tone, so that the temporal relationship between the visual S1 and the response could be varied. Even though stimulus–response integration was not highly sensitive to this temporal relationship, S1 was much more effectively integrated with the response if the stimulus appeared close to the execution of the response rather than when it was planned.

This suggests that the integration takes place close to response execution as well, presumably triggered by an evaluation of the response's success. It is this process that we think was affected by our valence manipulation. Given the strong evidence that stimulus–response learning is mediated by success-dependent depletion of dopamine (Schultz, 2002), our scenario is consistent with the idea that visuo-motor binding is under dopaminergic control. However, in the absence of converging evidence from more direct manipulations of dopaminergic activity in this is only a possibility.

Second, the valence manipulation was only effective when the task-relevant feature was shape (experiment 1) but not location (experiment 2) or color (experiment 3). In experiment 1, performing the task required subjects to direct their attention to shape, as this was the relevant S2 feature. If we assume that this attentional set was not disabled before and after processing S2, which is demonstrated by the observation that S1–R1 integration was impacted by which feature was relevant for S2, we can assume that the nature of this set affected the processing of the picture as well. Given that the identification of a picture's positive or negative valence requires the processing of shape information, it makes sense to assume that valence was determined only if shape was relevant but not if the attentional set was tuned to location and color, as in experiments 2 and 3. In other words, the processing of valence seems to rely on attention to shape, which is not consistent with previous claims that the extraction of affective information proceeds automatically and preattentively (e.g., Le Doux, 1996; Zajonc, 1980).

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