INVESTIGATING THE RELATIONS BETWEEN OBJECT AFFORDANCE AND PERCEPTION USING BEHAVIOURAL AND BRAIN IMAGING EXPERIMENTS

by

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ABSTRACT

Previous research has shown facilitatory effects on attention and perception when object pairs are positioned for action compared to when they are not positioned for action. The present thesis aimed to better understand the mechanisms underlying this paired-object affordance effect. Chapters 2 and 3 showed that different but interacting parieto-frontal networks contribute to the effects of paired-object affordance in healthy participants. Chapters 4 and 5 explored the effects of paired-object affordance on visual extinction; the data showed that recovery from extinction was sensitive to the familiarity of the object pair and the completeness of the active object rather than the passive object within an interacting pair. Finally, the role of contextual information and task demands on the automatic perception of paired-object affordance effects was directly explored. The results indicate that only explicit but not implicit task demands (searching for an action vs. a colour pair, respectively) had facilitatory effects on performance and that semantic information in a scene also modulates the automatic perception of paired-object affordance. The findings provide novel behavioural and neuroimaging evidence that paired-object affordance is influenced by contextual information and task demands, with the active object (the tool) within a pair modulating the allocation of attention.

To my parents, Norbert and Marianne,

Without whom none of my journey would be possible

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LIST OF ABBREVIATIONS

1PP	First-person perspective
3PP	Third-person perspective
ADM	Abductor digiti minini
AIP	Anterior intraparietal area
ANOVA	Analysis of variance
AON	Action observation network
AR	Action relation
Area F5	Pre-motor cortex
BCoS	Birmingham cognitive screen
EEG	Electroencephalography
EMG	Electromyography
FDI	First dorsalis interosseous
FFG	Fusiform gyrus
fMRI	Functional magnetic resonance imaging
FWE	Family-wise error
IFG	Inferior frontal gyrus
IPL	Inferior parietal lobule
IPS	Intraparietal sulcus
LH	Left-handed action
LOC	Lateral occipital complex
M1	Primary motor cortex
MEP	Motor-evoked potential

MNI	Montreal neurological institute
MNS	Mirror neuron system
MTG	Middle temporal gyrus
NAR	No action relation
PMC	Pre-motor cortex
RH	Right-handed action
RT	Reaction time
SD	Standard deviation
SE	Standard error
SEM	Standard error of the mean
SFG	Superior frontal gyrus
SMA	Supplementary motor area
SMG	Supramarginal gyrus
TMS	Transcranial magnetic stimulation

STATEMENT OF AUTHORSHIP

Chapters 1-7 contain material that has been published[1] or has been submitted[2] for publication to different academic journals. Accordingly, each of the five experimental chapters stands on its own. Based on this, there will be some background overlap across these chapters. To achieve a consistent format throughout the thesis, published and submitted papers have been changed accordingly. Although each published and submitted chapter is based on collaborative work, I am the primary author of these publications as I designed the experiments, and collected and analysed the data. Co-authors are my supervisors Glyn Humphreys and Pia Rotshtein because they commented and provided feedback on previous versions of each submitted paper. Joseph Galea is also a co-author for Chapter 3 because he provided feedback on data collection and data analysis as well as on the manuscript itself. Alexandra Stainton is also a named co-author of Chapter 6 because she helped with data collection and provided the data for two of the samples used in the study and contributed with feedback on the manuscript itself.

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[1] Chapter 4: Wulff, M. & Humphreys, G. W. (2013). Visual responses to action between unfamiliar object pairs modulate extinction. *Neuropsychologia,* 51, 622-632. doi:10.1016/j.neuropsychologia.2013.01.004

Chapter 5: Wulff, M., & Humphreys, G. W. (2015). Effects of broken affordance on visual extinction. *Front Hum. Neurosci., 9,* 515. doi:10.3389/fnhum.2015.00515.

[2] Chapter 2: Wulff, M., Humphreys, G. W., & Rotshtein, P. (submitted). Distinct neural effects of perspective and hand alignment on paired-object affordance: an fMRI study. *Cortex.*

Chapter 3: Wulff, M., Galea, J. & Rotshtein, P. (submitted). Paired-object affordance affects motor cortex excitability. *Cerebral cortex.*

Chapter 6: Wulff, M., Stainton, A., & Rotshtein, P. (submitted). Effects of paired-object affordance in search tasks across the adult lifespan. *Brain and Cognition.*

CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Vision plays an important role in interacting with the environment. Much of the evidence reviewed in this thesis indicates that, when we see objects (e.g., a cup, a knife, and a fork), we appear to automatically "know" what to do with them or how to use them. For example, we act to grasp a knife by its handle to spread butter on a toast or we use it together with a fork to cut a steak. How do these automatic responses happen? It is assumed that perception and action are not independent but are rather directly related to each other (Rizzolatti & Matelli, 2003). Supporting evidence for a direct linkage comes from the concept of *affordance*, proposed originally by J.J. Gibson (1979). The present thesis investigates how this direct linkage can be modulated by presenting two objects in different contexts, manipulating attentional allocation, and varying task demands. Each chapter will include a detailed review of the literature and the relevant theories. In the present introduction, I will primarily focus on reviewing concepts that are relevant to the entire thesis. I will start by discussing the affordance concept for single objects (section 1.2), then I will discuss affordance in relation to pairs of objects (paired-object affordance; section 1.3) and finish by presenting neurocognitive models related to affordance (section 1.4 and 1.5).

1.2 Affordance

Gibson (1979) first introduced the term affordance to describe the action possibilities an environment offers an animal – suggesting that, we perceive the world in terms of opportunities for action. What an object affords is determined by the physical properties of the object (e.g., shape, orientation, size) and shaped by the action capabilities of the agent. For example, a cup affords a power grip using both hands by a child, while this cup only affords grasping with one hand by an adult. The perception of affordance is also influenced by the action context in which an object is presented. Seeing a spoon next to a cup will afford a stirring action while a spoon next to a bowl will afford an eating action (the context modulation of affordances will be outlined in section 1.3). Furthermore, previous research has shown that the presence of a hand interacting with an object triggers or primes possible actions (e.g., Kumar, Riddoch, & Humphreys, 2013; Kumar, Yoon, & Humphreys, 2012). Thus, Gibson's concept of affordance can be extended to include the presence of a hand as an additional affordance cue to afford a corresponding motor response. In the present thesis, I will use the extended concept of Gibson's affordance, specifically the extensions of context and hand cues to the concept of affordance as well as their interaction are the focus of the thesis. Gibson's concept will be discussed first, followed by the extended concept of affordance, although in both cases the term affordance will be used. To avoid confusion, I will use the term *paired-object affordance* to refer to affordance effects offered by pairs of objects (see section 1.3).

Gibson (1979) proposed that affordances are perceived directly without the need to recognise the object first – thus postulating a direct link between perception and action. Accordingly, the physical properties of the object itself (its affordance) automatically generate a motor response, even when there is no motor response required. Affordance is typically measured using stimulus-response compatibility paradigms (Michaels, 1988). Here participants view graspable objects (e.g., cups) and they have to make speeded responses to object properties (e.g., the vertical orientation of an object). Compatibility effects (i.e., faster responses), as index of affordance perception, are observed when the task-irrelevant orientation of a graspable object matches the response hand. In a seminal study, Tucker and Ellis (1998) presented pictures of graspable objects with the object handle pointing towards the left or the right. Participants had to determine by left-right key presses whether an object was upright or inverted. The authors found that responses were faster when the required manual response (e.g., right button press) was congruent with the task-irrelevant orientation of the object’s handle (e.g., handle pointed to the right). This result is consistent with a motor response being automatically activated by the position of the task-irrelevant handle. Symes, Ellis, and Tucker (2007) supported that the task-irrelevant orientation of an object rather than the visually salient area of an object triggers the affordance effect. The authors presented artificial graspable 3D cylinders oriented to either the left or to the right. Note that these objects had not been previously associated with any action procedure (compared to household items such as a cup). Participants were required to make semantic decisions about the object’s texture using left-right button presses. Compatibility effects were observed when the orientation of the object corresponded with the response hand. Interestingly, compatibility effects were observed independent of whether attention was cued to the visually salient nearest or farthest area of the cylinder (Experiment 5). Symes et al. argued that the observed compatibility effect reflects affordance (i.e., orientation of the object) rather than attentional processing of the most salient or behaviourally relevant feature of an object (but see below for arguments for an attention-related hypothesis). Several other studies have demonstrated that affordance compatibility effects even occur when the object itself is task-irrelevant (e.g., responding to an imperative target superimposed on an object; Xu, Humphreys, & Heinke, 2015; Phillips & Ward, 2002) or regardless of which part of the object is attended (e.g., similar cueing effects were observed when the handle or the functional part of an object cued the location of a target; Vainio, Ellis, & Tucker, 2007).

To sum up, these data are consistent with affordances being evoked automatically, even when irrelevant to the task. Converging evidence has shown that the observation of graspable objects (i.e., tools) automatically activates action representations in corresponding motor areas, even in cases where no hand response actually needs to be made (for neuropsychological evidence, see e.g., di Pellegrino, Rafal, & Tipper, 2005; Riddoch, Humphreys, Edwards, Baker, & Willson, 2003; for experimental evidence, see e.g., Phillips & Ward, 2002; Tucker & Ellis, 1998; for neuroimaging evidence, see e.g., Grezes, Tucker, Armony, Ellis, & Passingham, 2003; Grafton, Fadiga, Arbib, & Rizzolatti, 1997).

However, recent evidence has cast doubt on the automatic perception of affordance as suggested by Gibson (for reviews, see e.g., Borghi & Riggio, 2015; van Elk, van Schie, & Bekkering, 2014; Thill, Caligiore, Borghi, Ziemke, & Baldassarre, 2013). Instead, there is growing evidence that affordance is sensitive to the task and the context. For example, affordance compatibility effects were absent when participants had to categorise objects (Netelenbos & Gonzalez, 2015; Derbyshire, Ellis, & Tucker, 2006) or when they had to make colour decisions (Pellicano, Iani, Borghi, Rubichi, & Nicoletti, 2010; Tipper, Paul, & Hayes, 2006). Tipper et al. (2006) suggested that the occurrence of compatibility effects require attention being directed to action-relevant object properties such as object orientation or size, while attention to action-unrelated features acts against the activation of affordance-related responses (but see, Vainio et al., 2007). Affordance perception is also influenced by contextual factors such as the location of the object in space (e.g., Costantini, Ambrosini, Tieri, Sinigaglia, & Committeri, 2010), the ownership of the object (Constable, Kritikos, & Bayliss, 2011), the presence of another person (Cardellicchio, Sinigaglia, & Costantini, 2013), the presence of other objects (e.g., Borghi, Flumini, Natraj, & Wheaton, 2012), and contextual information about action (e.g., the presence of a congruent or incongruent hand grip; Yoon & Humphreys, 2005). The latter two factors will be the focus of this present thesis and will be discussed in detail in the corresponding chapters. Taken together, the reviewed studies indicate that affordance perception is not automatic per se; instead affordances may be influenced by the task and contextual information. In Chapter 6, the role of task demands and context on the automatic perception of affordance was explicitly investigated by using an implicit (finding colour pairs) and an explicit (finding action pairs) visual search task.

In addition to the effects of task and context on affordance perception, there is also evidence that attention modulates affordance activation (Matheson, Newman, Satel, & McMullen, 2014; Kostov & Janyan, 2012; Handy & Tipper, 2007; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003; Anderson, Yamagishi, & Karavia, 2002). It has been suggested that tools bias attention based on the visual asymmetry created by the position of the handle, and this attentional capture towards the handle (the most salient part of an object) generates the motor response (Anderson et al., 2002; see also Cho & Proctor, 2010). In particularly, the handle of a tool rather than its functional end seems to bias visual attention (Matheson et al., 2014; for the opposite result see, van der Linden, Mathot, & Vitu, 2015; Roberts & Humphreys, 2011b). Using electroencephalography (EEG), Matheson et al. (2014) showed that the handle of a tool triggered an early visual attentional response in the extrastriate visual cortex, and argued that this early response is presumably elicited before a motor response in motor-related areas is activated (see also, Goslin, Dixon, Fischer, Cangelosi, & Ellis, 2012). A somewhat different approach to investigate attentional capture by the tool comes from Handy and colleagues (Handy & Tipper, 2007; Handy et al., 2003). In their EEG study (Handy et al., 2003), participants had to respond by button press to a target superimposed over a graspable or a non-graspable tool. The authors found an early visual attentional response (using event-related potentials) to task-irrelevant tools compared to non-tools when presented in the right visual field (i.e., the appropriate location for action). Handy et al. (2003) concluded that tools capture attention and argued for a right visual field dominance in visuomotor processing.

Further support for attentional capture by the tool comes from neuropsychological studies with patients suffering from visual extinction. Visual extinction, a neuropsychological disorder of attention, impairs the report of multiple items in the environment. Patients frequently fail to detect a contralesional stimulus when an ipsilesional stimulus appears simultaneously but they are able to detect a single contralesional stimulus when presented alone (Driver & Vuilleumier, 2001; Karnath, 1988). Di Pellegrino et al. (2005) presented cups with different handle orientations to parietal patients with visual extinction after right parietal brain damage. Patients reported the contralesional cup more often when the handle afforded a left-hand rather than a right-hand grasp. The authors proposed that action-relevant object features automatically capture visual attention by activating corresponding motor representations. Hence, patients with parietal lesions are nevertheless able to perceive affordance in the environment.

A link between affordance and attention can be also observed with pairs of objects affording a mutual action (e.g., pouring for cup and teapot). Presenting single objects in an action relationship next to another object (e.g., cup-teapot) modulates affordance, extending the notion of affordance beyond effects offered by single objects (cf. Gibson, 1979). The pairings of objects is of particular relevance for the present thesis and will be outlined next.

1.3 Paired-object affordance

There is now substantial evidence that perception and attention are facilitated when two objects afford a mutual action (cup-teapot) compared to when they are unrelated (e.g., cup-knife; e.g., Wulff, Laverick, Humphreys, Wing, & Rotshtein, 2015; Laverick et al., 2015; McNair & Harris, 2014; Wulff & Humphreys, 2013; Borghi et al., 2012; Roberts & Humphreys, 2011a; Roberts & Humphreys, 2011b; Yoon, Humphreys, & Riddoch, 2010; Humphreys, Wulff, Yoon, & Riddoch, 2010a; Adamo & Ferber, 2009; Green & Hummel, 2006; Riddoch et al., 2003). In a seminal study, Riddoch et al. (2003) demonstrated recovery from extinction in fronto-parietal patients when the left and the right stimulus were oriented in a way that implied a functional relation (teapot and cup are facing each other) or not (teapot and cup are facing away from each other). Riddoch et al. suggested that extinction is ameliorated by the affordance for action offered by the action relation between the objects (cf. Gibson, 1979). Riddoch et al. (2006; 2003) argued that action relations between objects implicitly influence visual attention: When an action (functional) relation between two objects exists, these objects can be automatically grouped together as an “action unit” and in turn, the exaggerated attentional bias to favour the ipsilesional stimulus in extinction patients can be overcome due to attentional allocation to both members of an action-related object pair simultaneously. Riddoch et al. also distinguished between active and passive objects in an action relation, with the active object (the tool) being the stimulus that is actively used in the action and passive objects the stimulus that is passively held during the action. On error trials, when patients correctly reported only one of two items, patients reported the tool rather than the passive object when the objects were oriented for action but not when they were not oriented for action, regardless of its location in space (see also, Wulff & Humphreys, 2015, 2013). The presence of an action relation biased which object was first attended, even though patients were not consciously aware that two stimuli were presented.

Recovery from extinction also occurred with unfamiliar object pairs, indicating that the presence of an action relation, rather than the familiarity with the action, is critical (Riddoch et al., 2006). In a follow-up study, Humphreys et al. (2010a) examined whether the affordance effect offered by functional object pairs is modulated by the perspective in which objects are presented and the way objects are grasped for using them. The authors used coloured photographs of objects being grasped by a hand (either congruent or incongruent with those premorbidly used by the patients), and the perspective of the person holding the object was manipulated (first-person perspective, 1PP vs. third-person perspective, 3PP). In line with Riddoch et al. (2003), patients showed less extinction when the objects were correctly positioned for action compared to when they were not. The novel result was that recovery from extinction was stronger when the objects were held in hands whose positions were congruent with those used premorbidly by the patients. On top of this, the effect was enhanced when the objects were seen from a 1PP rather than from a 3PP. In Chapter 4, using the same design as Humphreys et al. (2010a), the effects of action familiarity on paired-object affordance in extinction patients were further explored. More specifically, I tested whether recovery from extinction can also be observed with objects which are unfamiliar as a pair (e.g., corkscrew-cup). If yes, are the effects increased when the objects are held by a hand which corresponds with the hand one would normally use? Also, is the graspability of objects important for the affordance effect? More precisely, does it make a difference in recovery from extinction whether the tool or whether the passive object within an object pair has a broken handle? This question was explored in Chapter 5.

Beneficial effects of action relations on attention and perception have been also reported in healthy participants (e.g., Xu et al., 2015; McNair & Harris, 2014; Roberts & Humphreys, 2011a; Roberts & Humphreys, 2011b; Yoon et al., 2010; Roberts & Humphreys, 2010b; Adamo & Ferber, 2009; Green & Hummel, 2006; Bach, Knoblich, Gunter, Friederici, & Prinz, 2005). For example, participants were faster making action decisions about functional object pairs when the objects were correctly co-located for action compared to when they were not (Bach et al., 2005). Using an attentional blink procedure, assumed to measure the allocation of visual attention (Raymond, Shapiro, & Arnell, 1992), the role of attention on affordance perception was directly studied by Adamo and Ferber (2009) and McNair and Harris (2014). These two studies showed a reduced attentional blink when T1 (e.g., hammer) and T2 (e.g., nail) formed a functional pair, suggesting that functional relations between objects enhance attentional selection, and thus the report of the otherwise extinguished T2 item.

The particular role of the tool and its location within a functional pair has been highlighted in several studies. Similarly to neuropsychological patients, healthy participants show a preferential bias towards the tool rather than the passive object (Wulff et al., 2015; Laverick et al., 2015; Xu et al., 2015; McNair & Harris, 2014; Roberts & Humphreys, 2011a; Roberts & Humphreys, 2010b) and performance is better when the tool is aligned with the hand the participant would normally use to perform the action (Laverick et al., 2015; Xu et al., 2015; Roberts & Humphreys, 2011a; Yoon et al., 2010). This latter result indicates that affordance perception is sensitive to the hand-object alignment. The effect of hand-object alignment in the context of functional pairs was further explored in the present thesis. Specifically, Chapter 3 assessed whether the motor cortex is sensitive to the way functional pairs are grasped, comparing neutral and tilted-interactive hand postures.

Taken together, there is evidence that affordance effects are modulated by the context objects are presented in, with beneficial effects on perception and attention when two objects afford a mutual action and when these objects are congruently grasped and aligned with the hands an observer would use to perform such an action. However, it remains unclear what mechanisms underlie affordance effects for paired objects. Two factors have been suggested and these will be reviewed below.

1.3.1 Mechanisms underlying paired-object affordance

Humphreys and colleagues (for recent reviews, see Humphreys et al., 2013; Humphreys et al., 2010b) suggested that the affordance effect for paired objects might reflect two components: a visual response to the visual familiarity of the object pair (referred to as visual-based affordance) and a motor response to possible actions evoked by the objects (referred to as motor-based affordance). Humphreys and Riddoch (2007) proposed that the effects of action relation may reflect statistical learning of the spatial relations between objects. When two objects are frequently used together in action relative to when they are not, the co-occurrence statistics for this object pair will be increased and thus perceptual grouping and perceptual report of the stimuli will be improved (i.e., there should be less extinction in a patient with a spatial bias in attention; see also Humphreys et al., 2010b). Consistent with the visual-based affordance response, extinction is reduced when the depicted action is familiar and seen both from a 1PP and a 3PP (Humphreys et al., 2010a). On top of this, however, affordance effects are larger when objects are seen from a 1PP perspective and align with the hands the patients would typically use for the action (Humphreys et al., 2010a). Whether similar visual- and motor-based affordance responses also occur with unfamiliar object pairs was studied in Chapter 4.

The distinction, between visual- and motor-based components of the affordance effect also fits with data from healthy participants. For example, Roberts and Humphreys (2010a) showed that there was increased activity in visually-responsive areas of the brain (e.g., the lateral occipital complex, LOC) when action-related objects were presented (for a similar result using transcranial magnetic stimulation, TMS, see Kim, Biederman, & Juan, 2011). The activity in these brain regions is typically linked to object processing (Goodale & Milner, 1992). On the other hand, Kumar et al. (2012) reported enhanced activity over the motor cortex when participants viewed a hand congruently grasping an object compared with when an incongruent hand grasp was depicted (for fMRI evidence, see Yoon, Humphreys, Kumar, & Rotshtein, 2012). There was also increased desynchronisation in mu rhythm activity over motor regions for congruent compared with incongruent grasp conditions (Kumar et al., 2013). This increased desynchronisation is consistent with a stronger motor response to stimuli congruent with an action compared to when the stimuli were incongruent with an action. Furthermore, viewing action-related objects either congruently or incongruently grasped led to left lateralised activation in motor-related parieto-frontal regions, while unrelated object pairs activated parieto-frontal areas bilaterally; the bilateral activation probably reflects the diminished perception of affordance (Natraj et al., 2013).

In Chapter 2, the neural correlates of visual- and motor-based affordance responses to paired objects were investigated in healthy participants. The role of visual-based affordance cues was studied by manipulating the orientation of the objects to each other and the perspective in which the stimuli were presented, while motor-based affordances were examined by aligning the gripped objects either with the hands the participants would normally use to produce the action or the other hand (cf. Humphreys et al., 2010a). To further examine the role of visual- and motor-based affordance responses to paired objects, motor-evoked potentials (MEPs) induced by TMS over the primary motor cortex (M1) were recorded in Chapter 3. Here I assessed whether motor cortex excitability is affected by the context in which gripped objects are presented.

Gibson (1979) suggested that we directly perceive action possibilities when we view tools. This direct route from vision to action has been incorporated in the dual-route model from vision to action (Riddoch, Humphreys, & Price, 1989). This model will be discussed below.

1.4 Dual-route model from vision to action

The ability to interact with objects is crucial for everyday life. There is growing evidence that action knowledge about how to interact with objects or how to manipulate objects can be retrieved via two routes. Firstly, it is assumed that the retrieval of action knowledge relies on access to semantic knowledge (e.g., Ochipa, Rothi, & Heilman, 1992). For example, seeing a fork will activate the action eating by accessing previous semantic knowledge about forks. This indirect semantic route is mediated by temporo-occipital regions within the ventral visual stream associated with object representation (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). Secondly, access to action knowledge can be also mediated by the physical properties of the object (its affordance; cf. Gibson, 1979) which automatically activates action and motor procedures bypassing semantic knowledge (referred to as procedural knowledge). For example, the shape of a knife affords a cutting or spreading action using a power grip while the shape of a cup affords a drinking action using a precision grip. The direct route goes from the occipital to the parietal lobe (dorsal visual stream) associated with object use (e.g., Goodale & Milner, 1992). The indirect and the direct routes have been integrated into the dual-route model from vision to action (Riddoch et al., 1989), which assumes that action retrieval and object use are mediated by two separate routes.

The dissociation of impairments between optic aphasia and visual apraxia supports the existence of two separate routes from vision to action, one focusing on semantic knowledge (intact in visual apraxia, impaired in optic aphasia) and the other one supporting action procedures afforded by the structural properties of the objects (intact in optic aphasia, impaired in visual apraxia; Riddoch et al., 1989). However, converging evidence suggests that the direct and the indirect semantic routes are not entirely separate, instead they are linked (e.g., Wulff et al., 2015; Laverick et al., 2015; Mizelle, Kelly, & Wheaton, 2013; Osiurak, Jarry, & Le Gall, 2010; Silveri & Ciccarelli, 2009; Osiurak et al., 2008; Frey, 2007; Yoon, Heinke, & Humphreys, 2002; Bozeat, Ralph, Patterson, & Hodges, 2002; Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000; Buxbaum, Schwartz, & Carew, 1997). For example, Wulff and colleagues (Wulff et al., 2015; Laverick et al., 2015) showed that making action decisions and selecting objects for action required the involvement of both the direct and the indirect semantic routes from vision to action (cf. Riddoch et al., 1989). Wulff et al. (2015) also compared lesion locations between patients who were impaired when selecting real objects for action (e.g., fork-knife) with patients who were able to perform the task. Impaired patients relative to intact patients had lesions to dorsal fronto-parietal (direct route) and ventral anterior temporal (indirect route) regions. The authors suggested that lesions to both the direct and the indirect routes can impair the ability to select objects for action. In Chapter 6, I further investigated the relation between procedural and semantic knowledge on paired object selection using a touchscreen interface. I also assessed whether the retrieval of action knowledge is modulated by age.

1.5 Neurocognitive models related to affordance

The above cited research and the present thesis investigated affordance using single objects or pairs of objects, respectively. In these studies, static pictures of objects implying an action without depicting the actual action being executed were used. The aim of these studies was to explore the direct perception of affordance and its role on attention. Nevertheless, ideas about affordance are related to other theories linking perception and action such as (i) the tool network (Lewis, 2006), (ii) the action observation network (AON; Grafton, 2009), and (iii) the mirror neuron system (MNS; Rizzolatti & Fogassi, 2014). Even though all these models use objects/tools as stimuli, they all focus on different aspects of the perception-action coupling: The tool network focuses on tool use, whereas the AON and the MNS examine how we understand other people's actions. The link between affordance and these three models will be discussed next.

1.5.1 Tool-selective network

Over the last 10 years, it has been established that viewing tools, a special category of objects (Creem-Regehr & Lee, 2005) activates a distributed left-lateralised network including the pre-motor cortex (PMC; planning of tool-related actions), the posterior middle temporal gyrus (pMTG; semantic knowledge about tools and tool motion) and the posterior parietal cortex (representation of tool skills; for recent reviews, see Orban & Caruana, 2014; Beauchamp & Martin, 2007; for meta-analyses, see Lewis, 2006; Grezes & Decety, 2001). The activation of regions within both the dorsal and the ventral visual stream fits well with the proposal of Creem-Regehr and Lee (2005) that tools can be "processed for what they are, but also for how they can be used" (p. 457; see also e.g., Canessa et al., 2008; Noppeney, 2008; Johnson-Frey, 2004; Chao & Martin, 2000; Goodale & Milner, 1992).

The automatic activation of dorsal (pre-motor and parietal) areas when viewing tools, assumed to be involved in reaching and grasping (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), corresponds well with Gibson's affordance concept (1979). It has been suggested that the dorsal motor-related activations reflect the neural correlates of the affordance effect (Orban & Caruana, 2014; Thill et al., 2013; Grezes & Decety, 2002, see also Rizzolatti & Matelli, 2003, for the revised dorsal visual stream model). Specifically, the visual properties of tools such as their shape, size, orientation or graspability (encoded by the inferior parietal lobule, IPL; Maranesi, Bonini, & Fogassi, 2014) rather than conceptual knowledge associated with the tool have been suggested to be responsible for affordance perception (Vingerhoets, Vandamme, & Vercammen, 2009; but see Tucker & Ellis, 2004).

The tool network is strongly linked to tool use. Frey (2007) proposed that tool use relies on both sensory-motor and semantic representations (cf. Binkofski & Buxbaum, 2013; Chao & Martin, 2000). However, theories of human tool use are beyond the scope of the present thesis, and therefore will not be further discussed (for recent tool use reviews, see van Elk et al., 2014; Orban & Caruana, 2014; Osiurak et al., 2010; Lewis, 2006; Johnson-Frey, 2004; Johnson-Frey, 2003).

Interestingly, both viewing and using tools activates the same left-lateralised parieto-frontal network (e.g., Lewis, 2006). It has been suggested that these regions contain mirror neurons – neurons which discharge when an goal-directed action is performed as well as when an action is passively viewed (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). The MNS and its role in action observation and action execution will be discussed in section 1.5.3.

To sum up, the tool network is automatically activated during the observation of tools, and this may provide the substrate of a strong link between the visual perception of a tool and its perceived action potential.

1.5.2 Action observation network

While the tool network is automatically activated during the mere viewing of graspable objects, the AON is automatically activated during the observation of another person's action (for a meta-analysis, see Caspers, Zilles, Laird, & Eickhoff, 2010). The AON has been associated with action understanding by means of action simulation based on mirror neurons (Grafton, 2009). In other words, observing another person's action elicits simulation processes which depend upon the type of observed action (e.g., goal-directed vs. body-related actions). The AON comprises a bilateral distributed network including the inferior frontal gyrus (IFG), the PMC, the superior temporal sulcus and the IPL (Grafton, 2009, see also Caspers et al., 2010). Grafton (2009) stressed that the AON partly overlaps with areas involved in executing goal-directed actions (PMC and IPL; Grezes & Decety, 2001) and with areas containing mirror neurons (PMC and IPL; Rizzolatti & Craighero, 2004, see below). The shared neural representations between action observation and action execution are assumed to be the basis for understanding other people's actions and intentions (Rizzolatti & Craighero, 2004), which will be reviewed in section 1.5.3.

It has been shown that the observation of goal-directed hand/arm actions evokes somatotopic PMC and IPL activation (simulation), supporting a direct match between action observation and action execution (Buccino et al., 2001). Moreover, the activation of the AON (in particular the PMC and the IPL) is influenced by the motor repertoire of the observer (e.g., responding differentially to viewing a human being vs. a dog performing actions; Buccino, Binkofski, & Riggio, 2004) and the familiarity with the action (e.g., Gardner, Goulden, & Cross, 2015; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006; Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005).

In sum, the AON is a framework that can provide insights into the mechanisms underlying action understanding. However, although the AON can simulate simple actions and decode their intentions, more complex actions such as tool use may require the involvement of other areas beyond the AON (Grafton, 2009).

1.5.3 Mirror neuron system

There are several theories of how we understand the actions of others. The most influential theory is the mirror neuron account. Mirror neurons have been first discovered in the monkey’s pre-motor cortex (area F5; Gallese et al., 1996; di Pellegrino et al., 1992), and subsequently in the monkey’s anterior intraparietal area (AIP; for a review, see Fogassi et al., 2005). In both areas, mirror neurons respond to both when the experimenter performs a goal-directed action and when the monkey performs a similar action. The direct matching between action execution and action observation (the mirroring mechanism) is evident in both monkeys and humans, and it has been argued to be the neurophysiological mechanism underlying action and intention understanding (Rizzolatti, Fogassi, & Gallese, 2001; for reviews, see Rizzolatti & Fogassi, 2014; Thill et al., 2013; Molenberghs, Cunnington, & Mattingley, 2012; Rizzolatti & Sinigaglia, 2010; Fabbri-Destro & Rizzolatti, 2008; Buccino et al., 2004; Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996, but see Turella, Pierno, Tubaldi, & Castiello, 2009, for a critical review). More specifically, it is proposed that we recognise and understand other people’s actions and their intentions by automatically mapping the observed action onto our own motor representations ('motor resonance'; Rizzolatti & Fogassi, 2014; Rizzolatti et al., 2001). In this sense, our brain represents the actions of others in a similar way to how it represents our own actions. The mirror mechanism has been also associated with imitation learning (e.g., Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001; Jeannerod, 1994). However, as stated by Rizzolatti et al. (2001), there might be other possible mechanisms beyond the mirror mechanism which contribute to action understanding.

In contrast to the affordance concept which relates to action perception and sensorimotor representations while observing graspable objects, the mirror mechanism is concerned with the perception of others people’s actions and intentions elicited by goal-directed action stimuli (for reviews, see e.g., Avanzini et al., 2012; Ortigue, Sinigaglia, Rizzolatti, & Grafton, 2010; Perry & Bentin, 2009; Iacoboni et al., 2005; Buccino et al., 2004; Buccino et al., 2001; Iacoboni et al., 1999). The core regions of the human MNS are the precentral gyrus, the IFG and the IPL (Fabbri-Destro & Rizzolatti, 2008; Rizzolatti & Craighero, 2004), with the IFG mediating action intention understanding (Ortigue et al., 2010; Hamilton & Grafton, 2008; Iacoboni et al., 2005). Interestingly, the precentral gyrus (PMC) and the IPL (both dorsal stream areas) are assumed to be the neural substrates underlying affordance effects (e.g., Grezes & Decety, 2002). More precisely, so-called canonical mirror neurons in area F5 and the AIP fire to the mere observation of graspable objects and during grasping movements (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Murata et al., 1997), suggesting that these areas might be the neurophysiological basis of sensorimotor transformations, and thus grasping (and the extraction of the associated affordance; Jeannerod et al., 1995; for a recent review, see Turella & Lingnau, 2014).

As the observation of graspable objects (affordance) and goal-directed actions (mirror neurons) activates shared (PMC and IPL) and specific (IFG) neural representations, it is plausible that action goal understanding is mediated by both mirror and canonical neurons (note that the perception of action possibilities depends upon context/goal; cf. Bach, Nicholson, & Hudson, 2014), while understanding the intentions of another person's action might require additional activation of the IFG (which is beyond the concept of affordance).

An alternative framework for action understanding and action prediction is proposed by Bach et al. (2014). In their affordance-matching hypothesis, the authors argue that action understanding and action prediction is based on object knowledge – knowledge about an object's function and how it can be used, respectively. Accordingly, action understanding and action prediction is mediated by matching observed and predicted actions: a match between observed action and an object's typical function facilitates inferring the goal of an observed action, while a match between observed action and the correct manipulation of objects facilitates predicting actions. Bach et al. suggested that the role of mirror neurons is to confirm a previously predicted action, based on an object's affordance extraction of another person's action, probably mediated by canonical-mirror neurons, i.e., neurons that fire to both object presentation and to actions performed by others (Bonini, Maranesi, Livi, Fogassi, & Rizzolatti, 2014; but see, Uithol & Maranesi, 2014).

Taken together, the exact relation between affordance and mirror neurons is still unclear and requires further investigations (see Thill et al., 2013, for a comprehensive review between the relation of affordance and mirror neurons).

1.6 Overview of the thesis

The present thesis explored the mechanisms underlying paired-object affordance effects in different contexts and the effects of paired objects on perception and attention focusing on three main topics: (i) the relations between paired-object effects and visual- and motor-based affordances; (ii) the neural correlates underlying paired-object affordances and (iii) the effects of paired-object affordance in selecting objects for action in visual search tasks. Chapter 2 investigated the neural correlates underlying paired-object affordance effects using the same stimulus set and a similar design to Humphreys et al. (2010a). The data show that paired-object affordance is mediated by interactions between visual-based affordance cues associated with responses in occipito-parietal cortices and motor-based affordance cues associated with responses in frontal motor cortices. Chapter 3 further evaluated the role of motor cortices in paired-object affordance perception applying TMS over the left or the right M1. The results indicate that the right (non-dominant) M1 supports cognitive changes related to the processing of paired objects. Chapter 4 and 5 investigated the effects of visual- and motor-based affordance cue manipulations on recovery from visual extinction. Chapter 4 assessed whether recovery from extinction also occurs with unfamiliar object pairs (visual-based affordances), while Chapter 5 tested whether the effects of paired-object affordance require the involved objects to be graspable (motor-based affordance) by comparing performance on objects with intact (graspable) or broken (non-graspable) handles. The results indicate that both visual- and motor-based affordance cues contribute to paired-object affordance effects, with the magnitude of the effects being dependent upon visual familiarity with the object pairs and the completeness of the tool rather than the object that is acted upon. Chapter 6 looked at the relations between procedural and semantic knowledge when selecting pairs of objects for action among distracters using participants varying in age and using two different search tasks. Participants had to search either for an action pair in the explicit action task or for matching colour pairs in the implicit visual search task. The results show that paired-object affordances generate effects on explicit performance, highlighting the role of task demands in selection processes. Age influenced performance in the action task, with increased performance in middle-aged adults which then decreases in later life. Chapter 7 gives a summary of results, and suggests future studies based on the limitations of this thesis.

CHAPTER 2: DISTINCT NEURAL EFFECTS OF PERSPECTIVE AND HAND ALIGNMENT ON PAIRED-OBJECT AFFORDANCE: AN FMRI STUDY[1]

2.1 Abstract

Attention is facilitated when two objects afford a mutual action, with the effect of action boosted when object pairs are viewed from a 1PP rather than a 3PP and when objects are aligned with how they would be grasped for action. Two processes might mediate the affordance effect: a visual-based affordance response, which is affected by the orientation and position of the objects, and a motor-based affordance response, which is related to hand-object interactions. The present chapter examined the neural correlates of the paired-object affordance effect. Participants performed a one-back memory task while viewing pairs of objects aligned for right- or left-handed actions, presented from a 1PP or 3PP and positioned for action or not. Increased responses for objects correctly positioned rather than incorrectly positioned for action (reflecting visual-based affordance cues) were found in inferior parietal and superior-middle temporal cortices. This effect was enhanced when the objects were viewed from a 1PP. In contrast, motor-based affordance cues increased activity in the superior medial frontal gyrus (SmFG), with this response also being enhanced by 1PP stimuli. Responses to 1PP relative to 3PP stimuli were larger in the posterior cingulate and postcentral gyri. This chapter demonstrates that paired-object affordance arises from interactions between visual-based affordance cues associated with responses in temporo-parietal cortices and motor-based affordance cues associated with responses in frontal motor cortices.

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[1] Chapter 2 is an adapted version of Wulff, M., Humphreys, G. W., & Rotshtein, P. (submitted). Distinct neural effects of perspective and hand alignment on paired-object affordance: an fMRI study. *Cortex.*

2.2 Introduction

Interacting with objects is essential for everyday activities such as preparing a cup of tea or making a sandwich. Such activities commonly involve interacting with two objects at the same time – with one object (the active object) acting upon the other (the passive object; e.g., bottle opener and a bottle, respectively). Previous work has established that functional relations between objects facilitate attention and perception (e.g., Wulff & Humphreys, 2013; Borghi et al., 2012; Roberts & Humphreys, 2011a; Yoon et al., 2010; Humphreys et al., 2010a; Green & Hummel, 2006; Riddoch et al., 2003). It has been argued that perceptual facilitation arises from affordance cues present in the stimuli. Affordance is traditionally defined in terms of the physical properties of an object that potentiate specific actions directly (Gibson, 1979). Affordance is based not only on the shape and orientation of an object in space but also on the context in which the object is presented in. For example, a bottle will afford a pouring action when presented next to a glass but a filling action when presented next to a water tap. Potential actions can also be evoked by viewing a hand interacting with an object (Kumar et al., 2013; Kumar et al., 2012). Thus Gibson's concept of affordance (1979) can be extended to include the presence of a hand as an additional cue that potentiates an action. Whether the effects of a hand grasping an object are modulated by the same functional and neural processes as effects of the relative positioning of objects is unclear. Here we compared the neural correlates of the two types of affordance cues: visual-based affordance cues based on the spatial relations between objects and motor-based affordance cues based on hand-object interactions (for a recent review, see Humphreys et al., 2013).

There is accumulating evidence demonstrating that perception is affected by visual-based affordance cues. Green and Hummel (2006), for example, showed that object identification increased when a target (e.g., a glass) and a distracter (a jar) were positioned to afford a mutual action (pouring) but not when an unrelated but correctly positioned distracter was presented (see also Roberts & Humphreys, 2011a). Similarly, participants were faster to make action decisions when an object was presented in the context of another object that potentiated a mutual action compared to when it was presented next to an object which did not potentiate a mutual action (Borghi et al., 2012). Furthermore, the presence of a functionally related object can affect the kinematics for reaching, grasping and lifting a target object (De Stefani, Innocenti, Bernardi, Campione, & Gentilucci, 2012).

A similar advantage for interacting pairs has been found with neuropsychological patients. Riddoch et al. (2003) showed that attentional deficits were ameliorated when two objects were positioned in a way that afforded a mutual action compared to when the objects were unrelated. At the neural level, it has been suggested that visual-based affordance is mediated by temporo-occipital region (Roberts & Humphreys, 2010a). Enhanced activity in the lateral occipital complex (LOC) and the fusiform gyrus (FFG) was observed for interacting compared to non-interacting objects (see also Kim & Biederman, 2011). TMS applied to the right LOC disrupted object affordance effects raised from visual-based affordance cues (i.e., the effect of positioning objects next to each other; Kim et al., 2011; though see, Baeck et al. 2013). In contrast to the above studies, positioning tools for actions in correct functional pairs was associated with responses in but not limited to the ventral visual stream (Mizelle & Wheaton, 2010b). Mizelle and Wheaton (2010b) compared functional magnetic resonance imaging fMRI responses for correct and incorrect tool positions for action (tool grasp by a hand vs. placed on the table) and functional pairings (e.g., hammer-nail vs. hammer-mug, in both cases the objects were positioned to afford a mutual action). When the tool was positioned for action, irrespective of the functional pairing, increased responses were observed in a widespread network, including the posterior occipital gyrus and precuneus, middle and inferior temporal gyri, inferior and superior parietal gyri, and inferior and middle frontal gyri, with increased responses in this network for correct (familiar) compared with incorrect functional pairs. Furthermore, fMRI adaptation studies have been shown that occipito-parietal areas are sensitive to changes in object orientation but not to object identification (Niimi, Saneyoshi, Abe, Kaminaga, & Yokosawa, 2011; Valyear, Culham, Sharif, Westwood, & Goodale, 2006), with this orientation effect only being present when the objects were graspable (vs. non-graspable objects; Rice, Valyear, Goodale, Milner, & Culham, 2007). Taken together, these results suggest that an object grasped by a hand and positioned for action as part of a familiar functional object pair is coded by bilateral ventral (occipito-temporal) and dorsal (posterior occipital and superior parietal-frontal) visual pathways, with primarily involvement of the left inferior parietal cortex.

Motor-based affordance cues also enhance perception. Motor-associated responses are modulated by the way a hand interacts with an object. For example, action decisions are facilitated when objects are congruently (vs. incongruently) grasped (e.g., Wulff et al., 2015; Laverick et al., 2015; Borghi et al., 2012; Yoon & Humphreys, 2005). Participants are faster at making action decisions than semantic decisions when the object position matched the participant’s handedness (for a similar result with neuropsychological patients, see Humphreys et al., 2010a). Mizelle, Kelly, and Wheaton (2013) presented functional object pairs oriented for action with a correct or incorrect tool grip (e.g., the tool was grasped by its handle and the functional end of the tool was oriented toward the recipient of the action or not). For the correct tool grip, there was enhanced response in bilateral fronto-parietal and temporo-occipital cortices, while incorrect tool grip conditions activated bilateral superior and middle temporal cortices. Recently, we showed that lesions to bilateral pre-motor, left parietal and right temporal cortices were associated with reduced effects of grip congruency on action decisions (Wulff et al., 2015). An fMRI study showed increased activity in superior medial frontal, left inferior parietal and right superior temporal cortices for congruently gripped and acted upon objects compared to incongruent object use (Yoon et al., 2012). Enhanced EEG activity (Kumar et al., 2012) as well as reduced mu synchronization over the motor cortex (Kumar et al., 2013) has been reported when participants viewed a hand congruently grasping an object compared with when an incongruent hand grip was depicted (see also Petit, Pegna, Harris, & Michel, 2006). Hand alignment effects (i.e., whether the tool is held by the dominant or the non-dominant hand) have also been reported to modulate mu coherence over parietal and pre-motor regions, with coherence for contralateral observed tools (Kelly, Mizelle, & Wheaton, 2015). Reduced mu rhythm in the sensorimotor cortex has been associated with motor preparation (Pfurtscheller, Neuper, Andrew, & Edlinger, 1997) as well as with execution and observation of hand-object interactions (Muthukumaraswamy, Johnson, & McNair, 2004; Muthukumaraswamy & Johnson, 2004). Thus, when grip congruency is modulated by hand alignment (e.g., the left hand holding a tool) enhanced motor excitability has been reported for incongruent-misaligned (less common) hand grips. The opposite pattern can be observed when congruency is manipulated by the way a hand grasps the tool, with increased motor response for congruent grip conditions. In sum, these studies highlight the importance of frontal-motor regions in representing motor-based affordance cues, and specifically suggest that different motor cues (aligned vs. incongruent) may result in opposite pattern of activation.

Finally, the action observation literature highlights the importance of visual perspective (1PP vs. 3PP) in triggering sensory-motor representations. Watching video clips of actions from a 1PP elicits larger neural responses in fronto-parieto-occipital areas (e.g., precentral gyrus, postcentral gyrus, IPL, inferior occipital gyrus) than when the action is presented from a 3PP (e.g., Watanabe et al., 2011; Hetu, Mercier, Eugene, Michon, & Jackson, 2011; Hesse, Sparing, & Fink, 2009; Alaerts, Swinnen, & Wenderoth, 2009; Bruzzo, Borghi, & Ghirlanda, 2008; Jackson, Meltzoff, & Decety, 2006; Saxe, Jamal, & Powell, 2006; Chan, Peelen, & Downing, 2004; Vogt, Taylor, & Hopkins, 2003; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002), though other studies have not found any effect of perspective on performance or brain responses (e.g., Bortoletto, Mattingley, & Cunnington, 2013; Oosterhof, Tipper, & Downing, 2012; Anquetil & Jeannerod, 2007). Recently, Kelly et al. (2015) demonstrated opposite effects of tool alignment, with the dominant hand response being affected by perspective, suggesting that perspective plays a key role in modulating both visual- and motor-based affordance cues.

The combined impact of visual- and motor-based affordance cues was examined by Wulff and colleagues (Wulff & Humphreys, 2013; Humphreys et al., 2010a) in two neuropsychological studies of fronto-parietal patients with visual extinction. Most patients had right hemisphere lesions. The authors presented pairs of objects held by a hand. The objects were positioned to potentiate an interaction or not (facing each other vs. facing away from each other), presented from a 1PP or 3PP and were aligned or misaligned with the patients' pre-morbidly dominant hand. Recovery from extinction was increased when interacting objects were presented from a 1PP and when the objects were aligned with the hands the patient would typically use for the action (Humphreys et al., 2010a). This suggests that visual- and motor-based affordance cues have an interactive effect on attention and perception. Note that even though these patients have commonly damage to the right IPL (e.g., Chechlacz et al., 2013; Karnath, Himmelbach, & Küker, 2003), they remained able to respond to the effects of action. As suggested by (Humphreys et al., 2010a), it could be that the effects are driven by neural areas separate from these involved in spatial attention (e.g., the left IPL for processing hand-object interactions; van Elk, 2014; Buxbaum, Kyle, Grossman, & Coslett, 2007; Grezes & Decety, 2002).

In the present chapter, we investigated the combined effects of visual- and motor-based affordance cues on the neural responses to paired-object affordance with healthy participants. Visual- and motor-based affordance cues were manipulated using a similar approach to Humphreys et al. (2010a). Using congruently gripped functional object pairs in a full factorial design, we assessed whether the effects were driven by (i) visual-based affordance cues by manipulating the position of the objects to each other (correctly or incorrectly co-located for action, Figure 2.1) and/or (ii) the effects are driven by motor-based affordance cues by gripping the tool (active object) with the right or left hand. Thus, the active object could be either anatomically aligned or misaligned with the dominant hand. Finally, (iii) each functional pair was presented from a 1PP or a 3PP. We assumed that the perspective manipulation would trigger both visual- and motor-based affordance processing, as perspective effects have been reported for both action observation and tool use studies examining the effects of object orientation on performance (see above). Based on the neuropsychological data (Wulff & Humphreys, 2013; Humphreys et al., 2010a), we anticipated that in addition to the main effects of each affordance cue (i.e., action relation, hand alignment, and perspective) the three different experimental factors would interact. Specifically, we expected that viewing stimuli from the 1PP would increase the neural effects of the objects' co-location for action and hand alignment in the above predicted regions, as previously observed with neuropsychological patients. In line with previous literature, we anticipated that visual-based affordance cues would affect responses in occipito-temporal and occipito-parietal cortices; motor-based affordance cues would be primarily associated with responses in motor-associated areas in the frontal cortex while the combined effect of the various affordance cue types would be primarily observed in fronto-parietal motor areas.

2.3 Methods

2.3.1 Participants

Eleven right-handed healthy participants (two females; M_{age} = 65.09; SD = 12.14) were recruited from the volunteer panel at the School of Psychology, University of Birmingham. Handedness was determined by self-report. We recruited relatively older participants for two reasons: First we were interested in investigating the neural effects of paired-object affordance after extensive hands-on experience with tools; this experience is often lacking or very limited in the undergraduate student population who have limited experience with cooking or “do-it-yourself” tasks. Secondly, our cohort served as age-matched control participants for an fMRI study we ran with patients suffering from visual extinction which will be reported in a separate publication. Participants received £20 for their participation. Informed consent was obtained from all participants and the study was approved by the local Ethical Review Committee.

2.3.2 Stimuli

Thirty-two coloured photographs of common objects were used – the same as those in Humphreys et al. (2010a). Each photograph depicted an item grasped by a hand and held above a table, photographed from a 1PP and from a 3PP. The individual items for each perspective were combined into 16 object pairs that were commonly used together (e.g., bottle and bottle opener; see Figure 2.1a and Figure 2.1b for the 1PP and the 3PP, respectively). The two items were presented simultaneously, one on the right and one on the left side of fixation. We note that there were low-level visual differences between 1PP and 3PP stimuli, with 3PP stimuli in contrast to 1PP stimuli depicting more body parts due to the angle of the camera. However, there was no difference between correctly and incorrectly co-located object pairs for actions within each perspective condition, as the same pictures were used but their location was switched across conditions.

The experiment was a full factorial repeated-measures 2 x 2 x 2 design with the following factors: (1) the action relation between objects, the items were presented so that they appeared either to interact with each other (e.g., the bottle opener is about to open the bottle; referred to as action relation, AR) or not (e.g., the bottle is facing way from the bottle; referred to as non-action relation, NAR). (2) Hand alignment, the object pairs were positioned for right-handed or left-handed actions with the hands aligned or misaligned with those the participant would use to perform the action (referred to as RH and LH, respectively). Since we tested only right-handed participants, hand alignment was congruent for RH actions and incongruent for observing LH actions (e.g., for RH actions, the right hand holds the bottle opener while the left hand holds the bottle). Finally, (3) each object pair combination was presented from a 1PP or a 3PP. Note that from a 3PP the RH alignment is anatomically correct, while the LH alignment is mirror-matched correct (as if looking in a mirror).

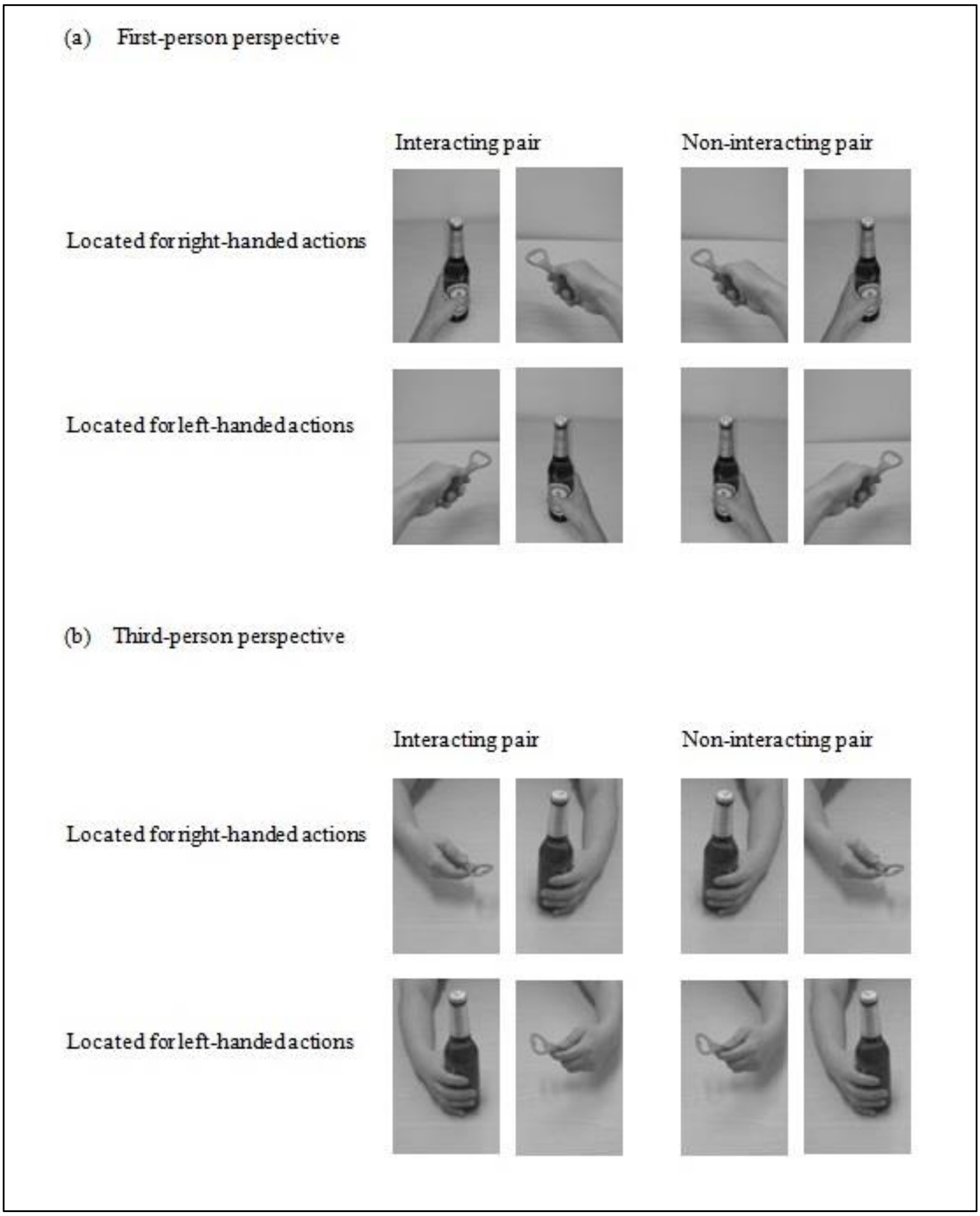

Figure 2.1. Examples of two-item stimuli presented from a first-person perspective (a), and from a third-person perspective (b). The objects were positioned as interacting pairs (left panels) or as non-interacting pairs (right panels). The active object (the bottle opener) was grasped either by the right hand (right-handed action; upper panels) or the left hand (left-handed action; lower panels).

2.3.3 Design and procedure

A similar design to Humphreys et al. (2010a) was used. Data for the two perspective conditions (1PP and 3PP) were collected in four separate runs on the same day, two runs for each perspective. The order of the perspective conditions was counterbalanced across participants, participants started either with the two runs of the 1PP or the 3PP. Each run contained thirty-two, 18s blocks, each block comprised of a separate condition (four blocks of each condition). In each block, we presented 18 object pairs at a 1Hz rate (700ms stimuli + 300ms fixation). In addition, 24 fixation-only blocks lasting 8s were pseudo-randomly interleaved between the experimental blocks to ensure they were relatively equally distributed across the experiment.

In all functional scans, participants performed a one-back working memory task. Participants were asked to press a response button with their right index finger whenever an object pair was identical to the one immediately preceding it. This task was chosen to ensure that participants maintained attention throughout the experiment. The repetition stimuli were relatively rare (12.5%), treated as catch trial and modelled separately in the fMRI design as regressors of no interest. Importantly, the trials of interest did not require a motor response, hence, any responses in motor-associated areas cannot be simply attributed to hand movements. Prior to the fMRI experiment, participants completed a practice block of 148 trials for each perspective to ensure adequate performance in the task; the stimuli on these practice trials were different from those employed in the experimental trials to avoid carry-over effects.

Stimulus representation was controlled by E-prime software (Version 2.1; Psychology Software Tools, 2006). Stimuli were projected onto a screen inside the fMRI scanner and viewed from a distance of approximately 65 cm via a head coil mounted mirror. Stimuli subtended 11.42° x 8.69° of visual angle and were located 0.86° on either side of central fixation. All stimuli were displayed on a black background.

2.3.4 fMRI data acquisition

Imaging data were acquired using a 3T Philips Achieva scanner (Philips Healthcare Systems, Eindhoven, The Netherlands) at the Birmingham University Imaging Centre. A T1-weighted 1 x 1 x 1 mm anatomical image was acquired for each participant (sagittal orientation, TE/TR = 3.8/8.5 s). EPI images were acquired using an eight-channel SENSE head coil with a sense factor of 2. Thirty-three axial oblique slices, 3.5 mm thick were obtained in an ascending order (TR/TE = 2000 ms/35 ms, 79.1° flip angle, 2.5 x 2.5 x 3.5 mm voxel-size, 240 x 240 mm^2 field of view). The scan included 4 dummy volumes; for the data we used 202 functional volumes per run. As the MRI scanner received a software upgrade in the middle of our data collection, five participants were scanned with a flip angle of 85°; the type of MRI sequence was included as a covariate of no interest in the statistical analysis (see below).

2.3.5 fMRI data analysis

Data analysis was performed using SPM 8 (Wellcome Department of Imaging Neuroscience, London; www.fil.ion.ucl.ac.uk/spm). The pre-processing steps included slice timing correction of all slices to the onset of the middle slice, spatial realignment and unwrapped (correction for head movements and distortions by head movement interactions; Andersson, Hutton, Ashburner, Turner, & Friston, 2001), co-registration of the mean EPI image to the T1-weigthed image. Normalization parameters for transforming the data to

Montreal Neurological Institute (MNI) space were computed on the T1 images using the advanced segment-normalise procedure (Ashburner & Friston, 2005). These parameters were applied to the EPI data and images were re-sliced to 3 x 3 x 3 mm voxels and spatially smoothed with a full width at half maximum Gaussian kernel of 9 mm to minimise inter-participant variability and adhere to the requirements of the random field theory (Worsley & Friston, 1995).

The General Linear Model was used for statistical analysis (Friston et al., 1995). First, we estimated the effect of each condition for each participant averaged across the two functional runs for each perspective by convoluting the canonical hemodynamic response function with the onset of each event of each condition [2 (perspective) x 2 (action relation) x 2 (hand alignment)]. We modelled separately the repetition events (catch trials) which included the participant's response to ensure that any motor response did not interact with our results. In addition, the six realignment parameters were included as regressors of no interest to account for movement-related variance. High-pass filtering (128 s) was used to increase signal-to-noise ratio by removing scanner and physiological noise.

To allow generalisation of the results, we used random effects analysis. Here we entered the images from all participants generated by the first-level analyses for each of the eight conditions (i.e., 2 x 2 x 2). In this analysis, we assumed dependency and unequal variance between the conditions. The two types of MRI sequences were modelled as a covariate of no interest to ensure that our results were not affected by these differences.

The analysis focused on three main effects: (i) the action relation, (ii) the perspective and (iii) the hand alignment. In addition, based on previous studies with neuropsychological patients where the 1PP boosted the effects of the action relation and hand alignment (Humphreys et al., 2010a), we examined the neural correlates that were associated with these simple effects: (i) 1PP: AR > NAR and (ii) 1PP: LH vs. RH. To ensure that the observed effects were specific to the 1PP and were not observed for 3PP stimuli, we used the corresponding interaction contrast as an inclusive mask at p < .05 (uncorrected): (i) 1PP: AR > NAR & 3PP: NAR > AR [i.e., (1PP_AR - 1PP_NAR) - (3PP_AR - 3PP_NAR)] and (ii) 1PP: LH > RH & 3PP: RH > LH, and vice versa, respectively. We used a similar approach to test for the neural correlates of objects correctly co-located for actions that were grasped by congruently aligned hands (active object in the dominant hand). We had a priori hypotheses regarding the expected sources of the interaction, and hence used simple effects to test these hypotheses; interaction as a mask was used to restrict the search space. For descriptive purpose of the main clusters of interests only, we extracted the parameter estimates (betas) from a 6-mm sphere around the cluster's peak and plotted these results in charts.

For all analyses, we used a family-wise error (FWE)-corrected threshold of .05 at peak/cluster-level. Using the FSL default, the voxel threshold was set to (T(10) > 2.37, p < 0.01). All results are reported in the MNI coordinate system. The anatomical labelling was done with the Anatomical Automatic Labeling toolbox (Tzourio-Mazoyer et al., 2002) and the Human Brain Atlas (Duvernoy, 1991). The approximately corresponding Brodmann's areas were determined using MRIcron software (http://www.sph.sc.edu/comd/rorden/mricron/).

2.4 Results

2.4.1 Behavioural results

The overall accuracy during the one-back task was 68%. The performances were reliably above chance, *t*(10) = 3.32, p = .008. Although the accuracy is relatively low, it does match a previous study with elderly participants (Laverick et al., 2015) using a one-back task performed on stimuli depicting hand-object interactions (mean = 75% ± 27% SD). We note, though, that in this study young and elderly participant’s performed similarly in terms of accuracy. It is difficult to explain why accuracy was relatively low. It may relate to the relative rarity of the catch trial targets, the relative high visual similarity of the stimuli (two hands holding two objects), or the age of the participants.

We next tested whether accuracy was affected by the conditions. The accuracy data were entered into three-way within-participant design ANOVA with the factors being perspective (1PP, 3PP), action relation (AR, NAR), and hand alignment (RH, LH). There was only a borderline interaction between action relation and hand alignment, F(1,10) = 5.52, p = .046). Surprisingly, although not significant participants tended to be more accurate when the interacting pair was presented for a left-handed vs. a right-handed action (typically the incongruent hand position for right-handed participants), *t*(10) = 2.17, p = .055, while there was no effect of hand alignment for non-interacting pairs (p = .402). Overall, importantly the results indicate that the task was equally difficult across the different conditions. This ensured that any observed results cannot be driven by differences in completing the task per se.

2.4.2 Imaging data

First we report the neural correlates of the main effects of action relation, perspective, and hand alignment (Table 2.1, Figure 2.2 - 2.4). Then we present the neural correlates associated with these simple effects (e.g., the interaction between action relation and perspective; Table 2.2 - 2.4, Figure 2.5 - 2.6). A schematic summary of the results is illustrated in Figure 2.7.

Table 2.1 Main effects of action relation, perspective and hand alignment

Region	BA	Cluster size	Peak-Z	MNI Coordinates (mm)		
				x	y	z
a) AR > NAR						
IPL	40	1158*	4.78*	-39	-40	55
Precuneus	23	381*	3.86	6	-52	31
STG extends to	21	474*	3.84	60	-28	1
MTG				54	-64	13
FFG				45	-46	-17
b) LH > RH						
SmFG	6	1062*	4.87	6	14	67
Hippocampus/PHG	30	391*	3.40	15	-25	-14
c) 1PP > 3PP						
Postcentral gyrus	3	340*	4.06	-18	-34	49
PCC	40	347*	3.78	21	-52	34

Note. AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action; BA = Brodmann’s area; IPL = inferior parietal lobule; STG = superior temporal gyrus; MTG = middle temporal gyrus; FFG = fusiform gyrus; PCC = posterior cingulate cortex; SmFG = superior medial frontal gyrus; PHG = parahippocampal gyrus.

* At peak/cluster-level p < .05 (FWE-corrected).

2.4.2.1 Visual-based affordance cues

The main effect of action relation (Table 2.1a, Figure 2.2). Increased neural activity for interacting relative to non-interacting objects was observed in left IPL (including the intraparietal sulcus, IPS, superior parietal lobule and the supramarginal gyrus, SMG). At a lower threshold, the right IPS (MNI: 33 -37 52; peak-Z = 4.04) showed a similar response pattern. Additional regions that were sensitive to the action relation were the right precuneus (extending to the cingulate cortex) and the right MTG/superior temporal gyrus (STG; extending into the FFG). We note that the precuneus was deactivated during the experimental conditions. This is a common activation pattern for this region, showing decreased activation during cognitive demanding tasks relative to rest (for a review, see Cavanna & Trimble, 2006). The reversed contrast did not show any above threshold responses.

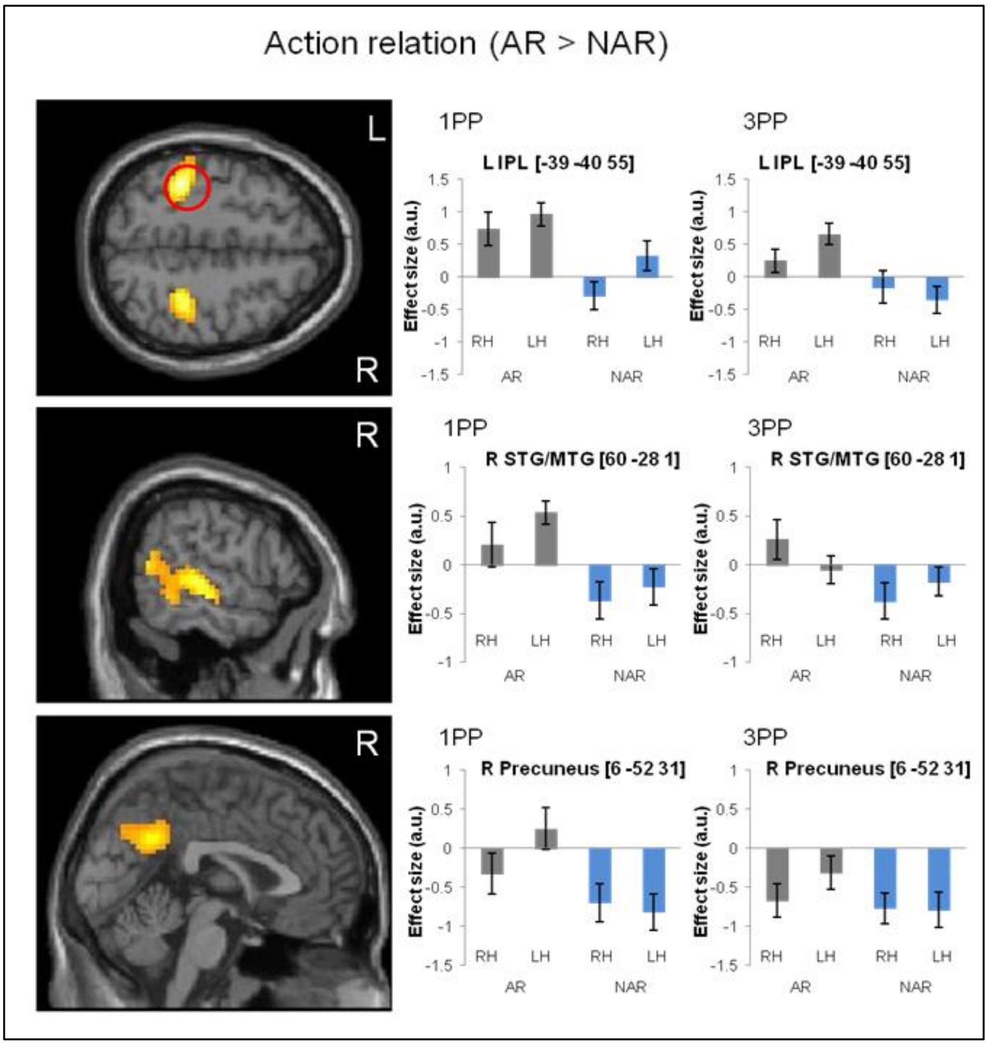

Figure 2.2. Activation foci for main effect of action relation (AR > NAR) were overlaid on a single-participant structural MNI-template (FWE-corrected p < .05; cluster defining threshold p < .01, uncorrected). The bar graph shows the averaged effect size extracted from a 6-mm sphere centred on the peak coordinate of inferior parietal lobule (IPL; circled in red), precuneus and superior temporal gyrus (STG)/middle temporal gyrus (MTG). Error bars show *SEM*s. Abbreviations: AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action.

2.4.2.2 Motor-based affordance cues

The main effect of hand alignment (Table 2.1b, Figure 2.3). There was enhanced activation for object pairs depicting left-handed actions vs. right-handed actions in the bilateral SmFG (extending to the superior frontal gyrus, SFG) and the right hippocampus (extending to the parahippocampal gyrus, the lingual gyrus and the globus pallidus). We note that the activation pattern in the SmFG cluster was similar across both perspectives, but the effects were stronger for 1PP than 3PP stimuli (see below for the interaction results and Table 2.2, Figure 2.5). There were no above threshold responses for the reversed comparison.

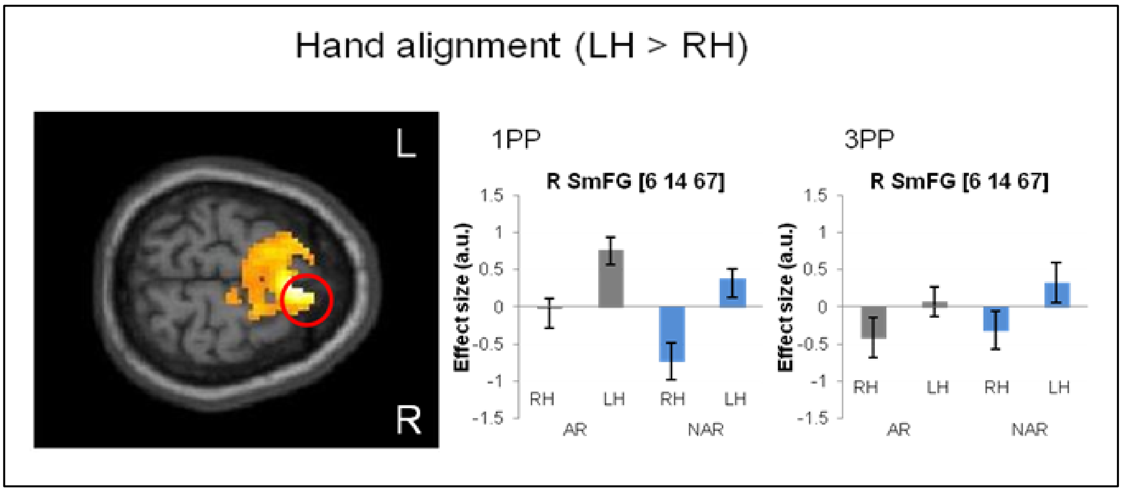

Figure 2.3. Activation foci for the main effect of hand alignment (LH > RH) were overlaid on a single-participant structural MNI-template (FWE-corrected p < .05; cluster defining threshold p < .01, uncorrected). The bar graph shows the averaged effect size extracted from a 6-mm sphere centred on the peak coordinate of superior medial frontal gyrus (SmFG; circled in red). Error bars show *SEM*s. Abbreviations: AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action.

2.4.2.3 Combined visual- and motor-based affordance cues

The main effect of perspective (Table 2.1c, Figure 2.4). Viewing pairs of objects from a 1PP vs. a 3PP resulted in activation in the left postcentral gyrus (extending to the middle cingulum) and the right posterior cingulate (extending to the IPS and precuneus). We note that these regions partly overlapped with the effects observed for objects correctly positioned for action (see above and Table 2.1a, Figure 2.2). There were no above threshold responses showing increased responses to 3PP vs. 1PP stimuli.

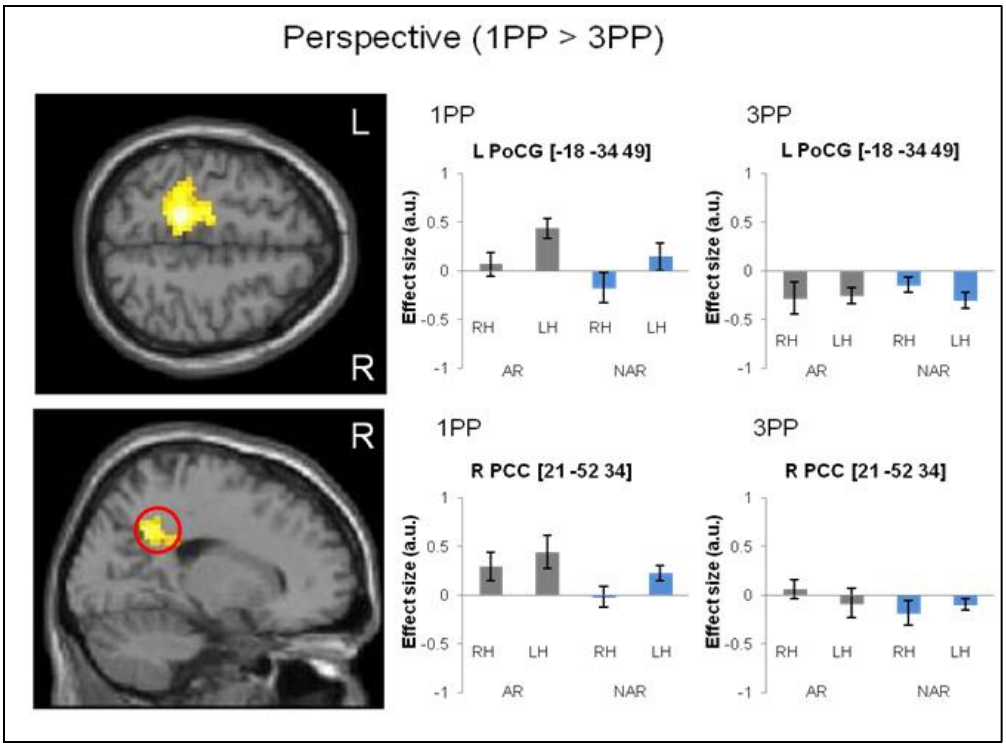

Figure 2.4. Activation foci for the main effect of perspective (1PP > 3PP) were overlaid on a single-participant structural MNI-template (FWE-corrected p < .05; cluster defining threshold p < .01, uncorrected). The bar graph shows the averaged effect size extracted from a 6-mm sphere centred on the peak coordinate of postcentral gyrus (PoCG) and posterior cingulate cortex (PCC; circled in red). Error bars show *SEM*s. Abbreviations: AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action.

The interaction between action relation and perspective (Table 2.2, Figure 2.5). Increased responses for interacting vs. non-interacting objects presented from a 1PP were observed in the left SmFG (extending to the SFG and the MFG), the left frontopolar cortex (extending to the anterior cingulate), the bilateral MTG (extending to the STG, the angular gyrus and the SMG), and the left posterior cingulate/precuneus. Note that the cluster involving the precuneus observed here, overlapped with the cluster showing a main effect for action relation (see above and Table 2.1a, Figure 2.2), suggesting the effect of action relation in this cluster was enhanced by the 1PP. Similarly, the interaction effect in the right MTG overlapped partly with the main effect of action relation (see above and Table 2.1a, Figure 2.2). Thus, the precuneus and the right MTG appear to process two different visual affordance cues driven by the orientation of the objects: spatial relation between objects (AR vs. NAR) and view point (1PP vs. 3PP).

Table 2.2 Common activation clusters for interaction between action relation and perspective (inclusive masking; $p < 0.05$, uncorrected)

Region	BA	Cluster size	Peak-Z	MNI Coordinates (mm)		
				x	y	z
[1PP: AR > NAR] incl. mask [1PP: AR > NAR & 3PP: NAR > AR]						
Frontal						
SmFG	9	490*	3.56	-9	47	52
Frontopolar cortex	10	382*	3.36	-9	59	16
Temporal						
MTG	21	740*	4.80*	-60	-49	4
MTG	22	115	4.68*	66	-37	4
Parietal						
Precuneus/PCC	23	943*	3.87	-6	-55	31

Note. AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; BA = Brodmann’s area; SmFG = superior medial frontal gyrus; MTG = middle temporal gyrus; PCC = posterior cingulate cortex.

* At peak/cluster-level $p < .05$ (FWE-corrected).

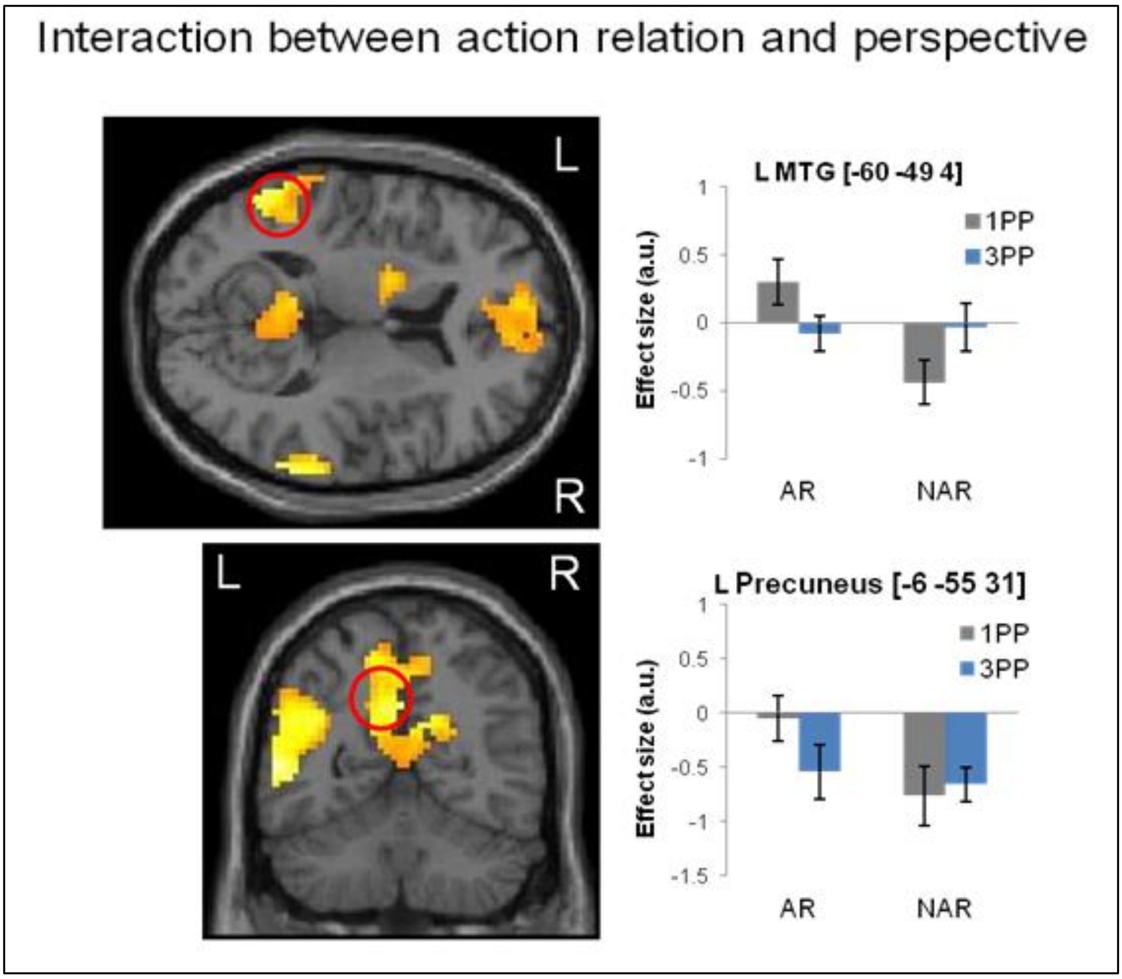

Figure 2.5. Activations for the action relation and perspective interaction using inclusive masking (p < .05), were overlaid on a single-participant structural MNI-template. SPM was threshold at p < .05 FWE-corrected; cluster defining threshold p < .01, uncorrected. The bar graph shows the averaged effect size extracted from a 6-mm sphere centred on the peak coordinate (circled in red) of middle temporal gyrus (MTG) and precuneus. Error bars show *SEM*s. Abbreviations: AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action.

The interaction between perspective and hand alignment (Table 2.3, Figure 2.6). Objects positioned for left-handed actions vs. right-handed actions presented from a 1PP activated the bilateral SmFG (extending to the postcentral gyrus), the left precentral sulcus and the left cerebellum (extending to the parahippocampal and the lingual gyrus). The interaction effect observed in the SmFG overlapped with the cluster showing a main effect of hand alignment (see above Table 2.1b, Figure 2.5), suggesting that the effect of hand alignment observed was facilitated when objects were viewed from a 1PP. There were no above threshold responses for 1PP stimuli when the tool was gripped by the right hand (right-handed action) vs. the left hand (left-handed action).

Table 2.3 Common activation clusters for interaction between perspective and hand alignment (inclusive masking; $p < 0.05$, uncorrected)

Region	BA	Cluster size	Peak-Z	MNI Coordinates		
				x	y	z
[1PP: LH > RH] incl. mask [1PP: LH > RH & 3PP: RH > LH]						
SmFG (extends to PreCS)	6	1693*	4.79*	3	17	64
PreCS	43	869*	3.85	-57	-1	25
Cerebellum		743*	4.16	-21	-70	-20

Note. 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action; BA = Brodmann's area; SmFG = superior medial frontal gyrus; PreCS = precentral sulcus.

* At peak/cluster level $p < .05$ (FWE corrected).

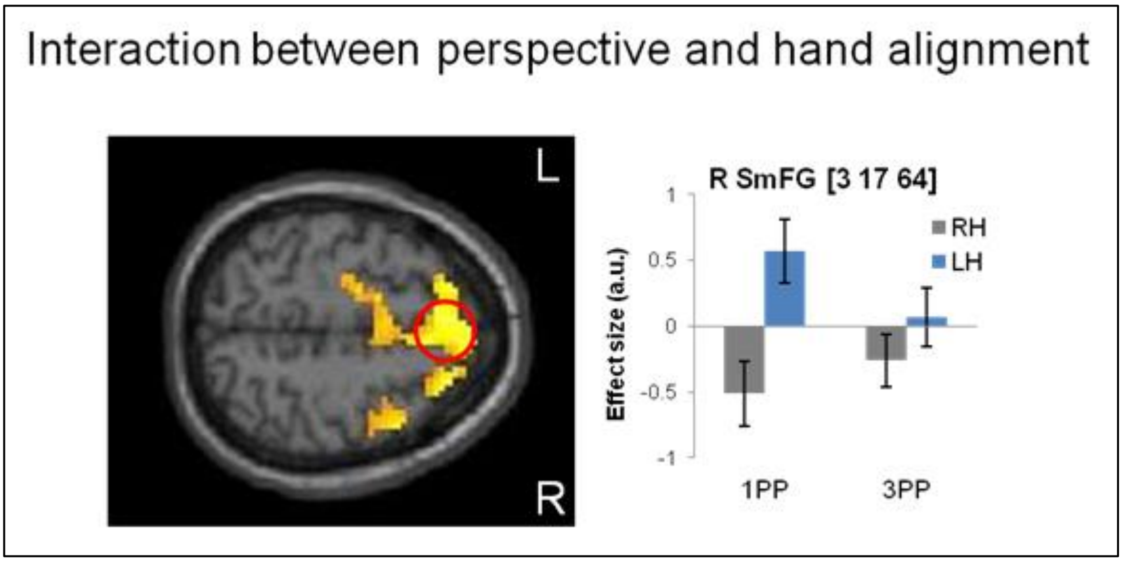

Figure 2.6. Activations for the perspective and hand alignment interaction using inclusive masking ($p < .05$) were overlaid on a single-participant structural MNI-template. SPM was threshold at $p < .05$ FWE-corrected; cluster defining threshold $p < .01$, uncorrected. The bar graph shows the averaged effect size extracted from a 6-mm sphere centred on the peak coordinate (circled in red) of superior medial frontal gyrus (SmFG). Error bars show *SEM*s.

Abbreviations: AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action.

The interaction between action relation and hand alignment (Table 2.4). When objects were correctly co-located for action and oriented for left-handed actions (vs. right-handed actions), there was activation in the left putamen (extending to the globus pallidus). There were no above threshold responses for correctly co-located stimuli when the tool was aligned for right-handed actions compared to when the tool was aligned for left-handed actions.

Table 2.4 Common activation clusters for interaction between action relation and hand grip (inclusive masking; $p < 0.05$, uncorrected)

Region	BA	Cluster size	Peak-Z	MNI Coordinates		
				x	y	z
[AR: LH > RH] incl. mask [AR: LH > RH & NAR: RH > LH]						
Putamen		121	4.72*	-27	-7	13

Note. AR = action relation; RH = right-handed action; LH = left-handed action; BA = Brodmann’s area.

* At peak/cluster level p < .05 (FWE corrected).

2.5 Discussion

The present chapter investigated the neural correlates of visual- and motor-based affordance cues contributing to paired-object affordance. We manipulated action relations between objects (visual-based affordance cues), hand alignment (motor-based affordance cues), and perspective (visual- and motor-based affordance cues). Figure 2.7 presents a schematic summary of the results. Action relations, associated with visual-based affordance, affected primarily responses along the dorsal route from temporal to inferior parietal areas.

Responses to hand alignment, assumed to reflect motor-based affordance, influenced activity in SmFG. The perspective manipulation modulated responses to visual-based affordance cues in inferior parietal areas and changed responses to motor-based affordance cues in the SmFG. Thus the perspective manipulation should be viewed within the context of both visual- and motor-based affordance cues. Together, the results suggest that paired-object affordance is mediated through visual- and motor-based affordance cues. The former one was associated with activity in temporal-parietal regions and the latter one with frontal motor activity but the two networks also interacted.

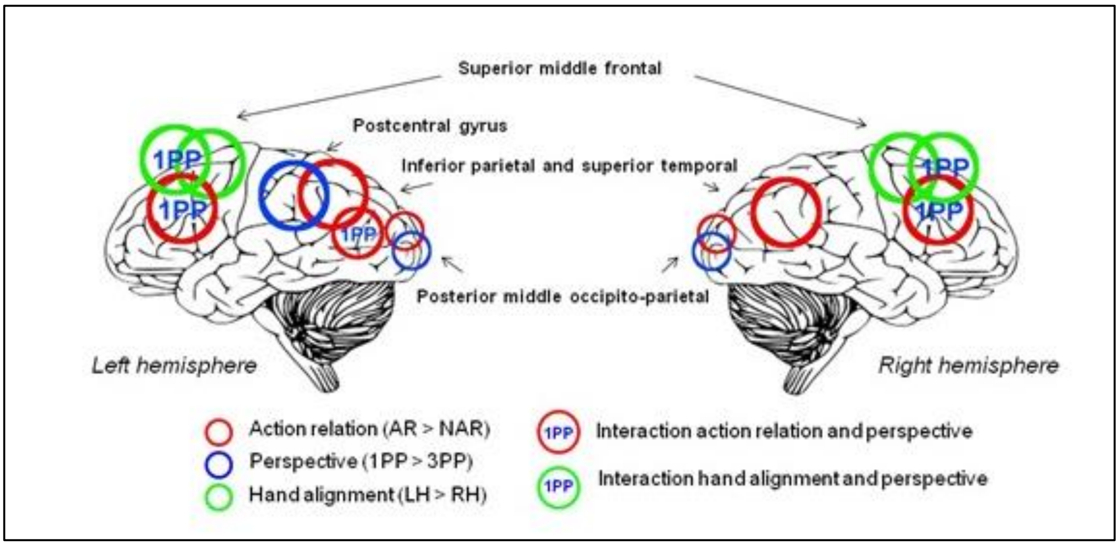

Figure 2.7. Schematic summary of the results. Abbreviations: AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action.

2.5.1 Neural correlates for visual-based affordance cues

The data suggest that a network of regions along the dorsal visual pathway is sensitive to the way objects are positioned. Specifically, bilateral inferior parietal cortices, right superior-middle temporal areas and precuneus showed stronger responses to correctly co-located objects for action, with the effect in these regions being enhanced when the objects were viewed from a 1PP. The precuneus and the MTG were sensitive to both the perspective and action relation manipulation as well as to their interaction.

The involvement of temporo-occipital regions in mapping action relations between objects as a function of their orientation and position is in agreement with the previous literature (Kim & Biederman, 2011; Kim et al., 2011; Roberts & Humphreys, 2010a). In line with Mizelle and Wheaton (2010b), we showed that viewing interacting objects activated not only temporal but also inferior parietal regions. The recruitment of parietal areas for correctly co-located (as opposed to incorrectly co-located) object for actions may seem contradictory to prior studies by Roberts and Humphreys (2010a) and Kim et al. (Kim & Biederman, 2011; Kim et al., 2011) who found only occipito-temporal activation for interacting object pairs. However, our study differed from these previous studies in several crucial aspects. Firstly, these previous studies used drawings of objects and not realistic pictures as in the present study (see also, Mizelle & Wheaton, 2010b). Recent studies have shown that the naming of realistic pictures compared to line drawings recruits more reliably the IPS (Valyear, Cavina-Pratesi, Stiglick, & Culham, 2007) and participants are faster to name photographs of tools than line drawings of the same implement (Salmon, Matheson, & McMullen, 2014). Secondly, in the study of Roberts and Humphreys (2010a) participants had to make a motor response for every trial, while in the present study motor responses were only required on catch trials. Thus, it is possible that the motor response preparation for every trial masked the more subtle effect of visual-based affordance on motor-associated cortices in Roberts and Humphreys' study. Finally, Mizelle and Wheaton (2010b) and we presented objects with a hand grip. There is compelling evidence that the presence of a hand affects responses in motor-associated areas, including the inferior parietal cortex associated with the processing of graspable objects (e.g., Lewis, 2006; Creem-Regehr & Lee, 2005; Grezes & Decety, 2001; Chao & Martin, 2000) and when observing hand-object interactions (e.g., Grafton, 2009). The predominately left IPL activity in the present study is consistent with the unilateral activation in the left IPL observed by Rumiati et al. (2004) when participants had to pantomime unimanual actions to visually presented objects (e.g., bottle opener) while controlling for perceptual, lexical, semantic, and motor processes. The authors suggested that the left IPL is the anatomical correlate of linking the visual properties of an object and its perceived action potential (i.e., its affordance; see also, Maranesi et al., 2014). We assume that this linkage is enhanced when objects are grasped by a hand. Taken together, we speculate that the additional activation of the left parietal cortex depends upon both the format of the stimuli and the nature of the task. Specifically, we suggest that the involvement of the dorsal pathway in processing visual-based affordance cues evoked by object pairs requires more realistic pictures of hand-object interactions.

2.5.2 Neural correlates for motor-based affordance cues

Responses of SmFG were affected by motor-based affordance cues (hand alignment), with these responses being magnified by 1PP stimuli. The SmFG (known as well as the supplementary motor area, SMA) has previously been reported during action observation, in particular when viewing graspable objects (for a recent meta-analysis, see Caspers et al., 2010; Grezes & Decety, 2002). It is also assumed that the SmFG has an important role in inhibiting response execution to object affordance – actions triggered by the visual properties of objects (Nachev, Kennard, & Husain, 2008). Lesions to the SmFG have been associated with the alien limb syndrome, in which the hand executes unintended actions, typically triggered by the environment (Della Sala, Marchetti, & Spinnler, 1991). Furthermore, patients with focal SmFG lesions showed deficits in automatic and unconscious inhibition of unwanted actions (Sumner et al., 2007).

In line with a recent EEG study by Kelly et al. (2015), we observed increased motor cortex responses for misaligned compared with aligned object pairs with respect to the preferred hand of the participant, with the effects being stronger for 1PP stimuli. Note that the effects were not reversed for 3PP stimuli and they were also not lateralized. In the present study, we did not observe any increased responses for aligned relative to misaligned hand conditions. The present results appear to be conflicting to previous behavioural findings with neuropsychological patients (Humphreys et al., 2010a) and healthy participants (e.g., Yoon et al., 2012) showing improved perception when object pairs were aligned (vs. misaligned) with the preferred hand use. One potential way of resolving this apparent discrepancy is to consider the impact hand alignment manipulation has on action familiarity. Seeing actions performed with the preferred hands is more common, and thus more familiar than seeing actions performed with the non-preferred hands especially in the 1PP. There is increasing evidence that action representations are influenced by novelty and sensorimotor experience, with greater activation for unfamiliar than for familiar actions (e.g., Plata Bello, Modrono, Marcano, & Gonzalez-Mora, 2014; Liew, Sheng, Margetis, & Aziz-Zadeh, 2013; Cross, Stadler, Parkinson, Schutz-Bosbach, & Prinz, 2013; Cross et al., 2012; though the opposite has also been reported, e.g., Gardner, Goulden, & Cross, 2015; Ruther, Tettamanti, Cappa, & Bellebaum, 2014; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006; Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005). It has also been shown that the less ‘automated’ an action is (e.g., using the left hand), the more widespread activities in motor-related areas can be observed (e.g., Schluter, Krams, Rushworth, & Passingham, 2001;

Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994). This effect was specifically observed in the SmFG, where unfamiliar but plausible functional object pairs elicited more responses than familiar and common action pairs (Hoeren et al., 2013).

In sum, we suggest that the SmFG may be involved more in inhibiting potential plausible actions that are less common. The same object pair is likely to evoke competing motor responses based on past experience and/or stored knowledge, with the less likely motor response being stronger inhibited. This may be part of the mechanisms that ensure that only plausible and intended actions are carried out, assuming that common and familiar actions are more likely to be intended. The results indicate that the behavioural effects of hand alignment might have arisen from an increase in motor inhibition triggered by the SmFG, leading to performance costs for aligned object pairs and performance benefits for misaligned objects. Clearly, further research is needed to clarify the role of SmFG and response inhibition in response to motor-based affordance cues.

2.5.3 Effects of visual perspective – combined visual- and motor-based affordance cues

We observed stronger response for 1PP versus 3PP in sensory-motor and posterior occipital-parietal cortices. The increased postcentral gyrus activity for 1PP stimuli is in line with previous neuroimaging (e.g., Hetu et al., 2011; Hesse et al., 2009; Jackson et al., 2006; Ruby & Decety, 2001) and TMS studies (3PP; Alaerts et al., 2009; Maeda et al., 2002). Jackson et al. (2006), for example, showed stronger involvement of sensory-motor cortices when the actor's perspective was congruent with the observer's own perspective. The 1PP advantage may arise because the observed action can be directly mapped onto the observer's own sensory-motor representations. In contrast, viewing actions from a 3PP may require spatial transformation to map the corresponding motor representations, and thus leading to weak or delayed representations (Jackson et al., 2006). Thus, the observed activity in the postcentral gyrus for 1PP stimuli reflects the congruence between the observed action and the participant which seems to be independent from low-level visual features differences (i.e., the amount of body parts depicted in each stimulus) between 1PP and 3PP stimuli. Though, it is plausible that low level differences between 1PP and 3PP conditions contributed to this effect. As discussed above, perspective also modulated effects of action relations in the MTG and precuneus and hand alignment in the SmFG. In both cases differential affordance effects were enhanced when objects were viewed from 1PP.

The observed results mirror previous behavioural findings with neuropsychological patients and healthy participants showing improved perception for correctly co-located objects for action (Yoon et al., 2010; Humphreys et al., 2010a; Riddoch et al., 2003), with the effect being enhanced when the objects were viewed from a 1PP (Humphreys et al., 2010a). This suggests that the perceptual advantages driven by visual-based affordance cues are mediated by regions along the dorsal pathway, with the precuneus and the MTG playing a key role in processing position and perspective affordance cues.

In the present study, we presented pairs of objects that afford an action without showing the actual action being executed. It is tempting to speculate how our present results relate to the AON (Grafton, 2009) and the mirror neuron system (MNS; Rizzolatti & Fogassi, 2014). An important theoretical and empirical difference between the two research fields is that object affordance research is concerned with the potential of actions initiated by the static environment specifically the shape and size of an object, while the AON and the MNS are associated with observing another person performing a dynamic action. Even though the task of the present study did not directly or explicitly require processing of the goal or the intention of the observed actions, implicit processing might have occurred. It is likely that an action goal was easier to perceive when objects were correctly positioned for action (‘goal-directed actions’) compared to when they were incorrectly positioned for action (‘non-goal-directed actions’). Thus, brain regions associated with goal understanding could have been also automatically activated when viewing static pictures of pairs of objects. In line with this assumption are the activations observed in the right MTG and the left IPL for action-oriented objects. These regions have been previously associated with understanding the intention of an observed action (e.g., De Lange, Spronk, Willems, Toni, & Bekkering, 2008) and the goal of an action (e.g., Hamilton & Grafton, 2006), respectively. However, in contrast to the AON and the MNS, viewing of paired objects did not activate inferior frontal and pre-motor cortices which are associated with the direct matching between action observation and action execution (the mirroring mechanism; Rizzolatti, Fogassi, & Gallese, 2001). Taken together, the present results indicate that affordance and action understanding have distinct and shared neural representations. Further studies are needed to provide further insights into the relation between affordance and action understanding.

2.6 Study limitations

In our stimuli an object was always depicted along with a hand. This may have led to overlapping visual-and motor-based affordance responses, and thus a strict dissociation between visual-and motor-based affordance cues with the present stimuli set is not possible. However, we suggest that the use of the term visual-based affordance cue is appropriate during the object’s orientation and position manipulation, as the observed effects are primarily driven by the perceptual properties of the objects; neural responses were found in regions along the dorsal pathway. In contrast, the presence of a hand evoked responses in motor-associated areas, suggesting that hand alignment primarily reflects a motor-based affordance cue. Taken together, the data indicate that paired-object affordance is driven by a combined and interactive effect of visual- and motor-based affordance cues, resulting in the recruitment of different but interacting neural networks.

The study had a relatively small sample size (11 participants). To increase statistical power, we used a within-subject block design associated with a high signal-to-noise ratio (Friston, Zarahn, Josephs, Henson, & Dale, 1999). Furthermore, to assess the strength of the evidence for the observed results, we computed a Bayes factor for each of the reported effect. The Bayes factor is based on the mean and variability of the measure. Using the response of the 6-mm sphere around the reported cluster’s peak, we found that for all reported peaks the Bayes factor was higher than 1.26. This means that the peak height provides weak to moderate evidence for the observed effect size. We note, though, that our main reliability assessment relied on thresholding the data at the cluster-level. However, since cluster-level reliability is not based on variability between participants, we could not use this measure in assessing the strength of the evidence or the study power. Taken together, although we only report data that survived FWE-correction, suggesting that the findings do not support a null hypothesis (no difference between conditions), we still need to exert caution when considering the size of the above reported effects (i.e., peak height) as these may be overestimated.

2.7 Conclusion

The present chapter demonstrate that both visual- and motor-based affordance cues contribute to paired-object affordance. Visual-based affordance cues (manipulated by changing the orientation and position of objects) were processed in left inferior parietal regions, while motor-based affordance cues (based on hand alignment) led to increased activity in the SmFG. The perspective manipulation increased responses to both visual- and motor-based affordance cues. The results suggest that paired-object affordance is mediated by different but interacting neural networks.

CHAPTER 3: PAIRED-OBJECT AFFORDANCE AFFECTS MOTOR CORTEX EXCITABILITY[1]

3.1 Abstract

The previous chapter revealed that paired-object affordance is mediated by different but interacting bilateral parieto-frontal networks. The present chapter further explored the role of M1 in paired-object affordance. More specifically, it was investigated whether left and right M1 excitability is modulated by the position of functional object pairs using TMS-induced MEPs. Right-handed participants observed object pairs in three hand contexts: no hand, held with a neutral or with a tilted-interactive hand posture. The hand posture implied action relation when the hands were facing each other but not when the hands were facing away. The objects were aligned for right- or left-hand actions. Reliable effects were only observed in the non-dominant (right) hemisphere. MEPs were greater for action-oriented objects aligned for non-dominant (left) vs. right-hand actions. For non-action oriented objects, an effect of hand posture was observed, with lower MEPs for left-hand actions when the hand posture was tilted compared to when it was neutral. The results indicate that the excitation of the non-dominant (right) M1 was influenced by action relation, hand alignment and hand posture, with stronger responses when the tool was gripped by the non-dominant hand and when the objects were action-oriented. The data suggest that M1 excitability is modulated by cognitive processes supporting paired-objects affordance.

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[1] Chapter 3 is an adapted version of Wulff, M., Galea, J. & Rotshtein, P. (submitted). Paired-object affordance affects motor cortex excitability. *Cerebral cortex.*

3.2 Introduction

Everyday activities such as making a cup of tea typically involve interacting with objects, linking perceptual and motor systems. There is accumulating evidence that objects engaged in a functional relation (e.g., knife and fork) facilitate attention and perception (McNair & Harris, 2014; Wulff & Humphreys, 2013; Borghi et al., 2012; Roberts & Humphreys, 2011a; Yoon et al., 2010; Humphreys et al., 2010a; Adamo & Ferber, 2009; Green & Hummel, 2006; Riddoch et al., 2003). However, less is known about the modulation of the motor system when seeing interacting object pairs. Within an object pair, the affordance "values" are often asymmetric, with the tool (the active object) typically acting upon the other (passive) object to produce the action (cf. Riddoch et al., 2003). Hence it is plausible that interacting object pairs compared to non-interacting object pairs are potentially associated with a stronger involvement of the motor cortex. Here we asked whether the excitability of M1 is modulated by hand-object interactions in the context of functional object pairs. More specifically, the present chapter investigated the extensions of context and hand cues to the concept of affordance as well as the interaction between them on the excitability of the motor system.

Previous research has shown that the observation of others performing or interacting with an object compared to the single object observation excites the motor cortex (for a recent review, see Naish, Houston-Price, Bremner, & Holmes, 2014; see also, Natraj et al., 2013; Kumar et al., 2012; Meister, Wu, Deblieck, & Iacoboni, 2012; Perry & Bentin, 2009; Prabhu et al., 2007; Rizzolatti et al., 1996; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Motor resonance is evident when the same muscles in the observer are excited as those involved when executing the same action (e.g., Leonard & Tremblay, 2007; Montagna, Cerri, Borroni, & Baldissera, 2005; Maeda et al., 2002; Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Fadiga et al., 1995). This implies a direct matching between observation and execution

(Gallese et al., 1996). There is also some evidence for a hemispheric asymmetry in motor control, with the right (non-dominant) pre-motor cortex being more strongly activated during the observation of bi- compared to unimanual actions (Heitger, Mace, Jastorff, Swinnen, & Orban, 2012; see also, van den Berg, Swinnen, & Wenderoth, 2010), while no strong lateralisation has been also reported (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006). Of particular relevance to the present study are the effects of grip congruency and object affordance cues (e.g., orientation, size) on motor resonance. Mounting evidence suggests that the motor cortex is sensitive to grip congruency, i.e., the familiarity/correctness by which a hand interacts with an object (e.g., Kumar et al., 2013; Kumar et al., 2012; Cesari, Pizzolato, & Fiorio, 2011; Grezes et al., 2003; Binkofski et al., 1999). It has been shown that viewing appropriately compared to inappropriately gripped objects modulated EEG activity over the central sulcus (Kumar et al., 2012; Petit et al., 2006) as well as increased mu de-synchronisation in pre-motor and motor cortices (Kumar et al., 2013). Neuroimaging and lesion analysis have also demonstrated the involvement of the pre-motor cortices in processing grip congruency (Wulff et al., 2015; Yoon et al., 2012). At a behavioural level, studies have reported better performance at making action decisions for appropriately compared to inappropriately gripped objects (Wulff et al., 2015; Laverick et al., 2015; Borghi et al., 2012; Yoon & Humphreys, 2005).

Object affordance cues, in the absence of a hand, also affect motor resonance. Buccino Sato, Cattaneo, Roda, and Riggio (2009) reported left M1 excitability for right hand but not left hand oriented objects, with the effect diminished when the affordance of the object was violated by presenting the object with a broken handle (for EEG evidence, see Drew, Quandt, & Marshall, 2015; Goslin et al., 2012; though see, Lien, Jardin, & Proctor, 2013; Cardellicchio, Sinigaglia, & Costantini, 2011, for failed replications of hand alignment effects). Behaviourally, performance was facilitated when the object location matched the response hand (Vankov & Kokinov, 2013) or the preferred hand of the participant when performing an action (Yoon et al., 2010; Humphreys et al., 2010a). Taken together, these results suggest a strong link between the action-related properties of an object and the corresponding motor response (cf. Gibson, 1979).

Note that the effects of grip and alignment as reported above were investigated using single objects rather than multiple objects. However, in everyday life we are surrounded by multiple objects which can form functional relations with each other (e.g., hammer-nail). A few behavioural studies have examined the combined effects of functional relations between objects and hand alignment on attention (Wulff & Humphreys, 2015, 2013; Yoon et al., 2010; Humphreys et al., 2010a). For example, patients with right fronto-parietal lesions and visual extinction were better at detecting objects positioned for action when the objects were viewed from a 1PP and when they were aligned with their preferred hands (Humphreys et al., 2010a). Wulff, Humphreys, and Rothstein (2014) recently tested the neural correlates underlying paired-object affordance in healthy participants using the same stimulus set as in Humphreys et al.'s study (2010a). The authors showed that the activity of the left pre-motor and primary motor cortex for object pairs positioned for action and viewed from a 1PP was sensitive to the alignment of the objects with the observer's effectors.

The present study was designed to further investigate the involvement of motor cortex, and specifically motor resonance when viewing functional object pairs in different action contexts. To do so, TMS was applied over left or right M1 and MEPs from the first dorsalis interosseous (FDI) and the abductor digiti minini (ADM) of right-handed participants were recorded while they observed functional object pairs. Motor resonance was assessed by presenting the objects aligned for left- or right-hand actions (i.e., the tool was gripped with the right or left hand, respectively). We also included three grip manipulations: (i) not grasped by hands, (ii) held with a neutral or (iii) a tilted-interactive hand posture. This was done to increase the “potential for action” in the viewed pairs. We assumed that tilted-interactive grips would elicit a stronger potential for action than neutral grips, whereas the neutral grip condition would evoke a higher potential for action than the no grip condition. Furthermore, we expected different FDI and ADM muscle activity when participants viewed tilted-interactive and neutral hand postures, with higher FDI muscle activation for tilted-interactive postures due to increased force requirements of the FDI while FDI and ADM should be equally involved when viewing neutral hand postures (for a recent review of muscle specificity, see Naish et al., 2014). We also manipulated the hand-object posture for gripped objects to imply an action relation between objects or not. A mutual action (e.g., hammering) was afforded when the hands were facing towards each other (referred to as action relation), while no mutual action was implied when the hands were facing away from each other (referred to as non-action relation). In line with the motor resonance idea, we anticipated that the lateralised M1 responses would reflect the hand that grasps the active object in the pair (e.g., stronger excitability in right M1 for left gripped tools). The effect is assumed to be enhanced for action-oriented objects and for tilted-interactive hand postures (stronger affordance cues).

3.3 Method

3.3.1 Participants

Eighteen right-handed participants (13 females; mean age = 20.4, SD = 3.0) from the University of Birmingham took part in the study. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971); the Mean Laterality Index (LI) was 89.0 (SD = 17.1). Participants received cash or course credits for their participation. All participants reported normal or corrected-to-normal vision. None of the participants reported any neurological or psychiatric impairment, nor did they have any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009; Wassermann, 1998). Informed consent was obtained from all participants and the study was approved by the local Ethical Review Committee.

3.3.2 TMS and MEP recording

Participants wore a cap and sat relaxed in front of a computer screen with the arms and hands rested on a table. TMS pulses were delivered using a 70-mm diameter figure-of-eight coil (Magstim Rapid, Whitland, UK). The coil was placed tangentially to the scalp with the handle pointing backward at a 45° angle with respect to the anterior-posterior axis. For each participant, the motor “hot spot” for the FDI in both motor cortices was determined by roughly 20 single pulses of TMS delivered at a supra-threshold stimulus intensity. After that, the resting motor threshold for the FDI muscle, defined as the minimum TMS intensity that evokes a MEP of greater than 50 µV in at least 5 out of 10 consecutive trials, was determined

(Rossini et al., 1994). This spot was marked on the cap to ensure a consistent coil position throughout the experiment; the coil was held in place manually by the experimenter (MW). The intensity of the TMS was then adjusted to evoke consistently an MEP of approximately 1 mV in the first session. This intensity was used for both the right and left M1 stimulation session.

We note that the intensity of the TMS needed to evoke a 1 mV MEP is typically weaker for the dominant (left) relative to the non-dominant (right) hemisphere (e.g., Hammond, 2002; Macdonell et al., 1991). The reason for keeping the TMS intensity (rather than the MEP amplitude) constant across motor cortices was to ensure that the stimulated hemisphere would not be confounded by the intensity of the stimulation within a participant (cf. Maeda, Keenan, Tormos, Topka, & Pascual-Leone, 2000). Furthermore, it also allowed us to explore the differences in stimulation intensities within each hemisphere. To ensure session order did not act as a confound, session order was included as a covariate in all analyses (see below).

Within the first session of the present study, when TMS was applied to the left (dominant) hemisphere, the required intensity to elicit a MEP was marginal lower than when TMS was applied to the right (non-dominant) hemisphere in the first session, $t(8) = -2.25$, $p = .055$. The stimulation intensity across participants ranged between 54% and 78% of the maximum stimulator output for the left M1 (mean 65%: SD = 8.26) and between 60% and 82% (mean 68%: SD = 7.53) for the right M1.

MEPs were recorded simultaneously from the FDI and the ADM muscles of the contralateral hand with disposable self-adhesive surface electrodes (Henleys Medical Supplies Ltd.). The active electrodes were placed over the muscle belly of both FDI and ADM muscles and the reference electrodes over the tendon of both muscles. The electromyographic (EMG) data were recorded approximately 500 ms before and after the TMS pulse to control for preactivation and background activity. MEPs were amplified (1000x) and filtered (20-1000 Hz) using 1902 quad system amplifier (CED 1902, Cambridge Electronic Design, Cambridge, UK), sampled (5 kHz; CED 1401), and then recorded by a computer using Signal software (Version 4.08; Cambridge Electronic Devices, Cambridge, UK) and stored for off-line analysis.

3.3.3 Apparatus and stimuli

Thirty coloured pictures of common household objects were used (Table 3.1). Each object was photographed from a 1PP using three grip conditions: (i) no hand grip, (ii) a neutral hand posture (the gripped object faced away from the observer) and (iii) a tilted hand posture (the gripped object faced towards a possible recipient; see Figure 3.1). Note that in both grip conditions the objects were grasped appropriately for object use. In the no hand grip condition, we presented the objects alone in a neutral position (the objects did not afford a particular hand grip). The no hand grip condition was identical to the neutral hand posture condition with the exception that no hand was present; the no grip and the neutral posture condition were analysed separately to assess the effect of hand presence on motor excitability. All images were horizontally flipped in Microsoft Office Picture Manager (Version 12) to create the mirror image of each item.

The individual gripped objects were combined into 15 functional pairs (Table 3.1, Figure 3.1) positioned for (i) a right-hand action (active object on the right side, passive object on the left side) and (ii) a left-hand action (active object on the left side, passive object on the right side). These two conditions were depicted with the objects either implying a mutual action or not, resulting in ten conditions [Action relation (oriented for action, not oriented for action) x

Posture (neutral, tilted) x Alignment (positioned for a right-hand or for a left-hand action)]. Note the factor action relation was only manipulated when a hand was present (see Figure 3.1.). In the no hand condition, we presented the objects aligned for right- or left-hand actions but in both cases the objects were oriented for action. The two items were presented simultaneously, one on the right and one on the left side of fixation.

E-prime software was used for stimulus presentation and the timing of the TMS (Version 2.0; Psychology Software Tools, 2006). The stimuli were presented on an 18-inch monitor (spatial resolution of 1024 x 768 pixels, frame refresh rate 60 Hz). The stimuli subtended 10.29° x 8.56° of visual angle and were located 0.86° either to the left or right side of central fixation.

Table 3.1 Object pairs used in the study

Active	Passive	Action familiarity rating (SD)
Peeler	Potato	2.06 (1.11)
Bottle opener	Bottle	2.50 (1.04)
Paint brush	Paint pot	3.00 (1.28)
Whisk	Bowl	3.39 (1.29)
Knife	Fork	3.44 (1.29)
Scourer	Washing up liquid	3.72 (0.96)
Tin opener	Tin	3.78 (1.17)
Teapot	Cup	3.94 (1.21)
Screw driver	Screw	4.00 (1.24)
Tea spoon	Coffee jar	4.17 (0.92)
Scissors	Paper	4.17 (1.15)
Spatula	Frying pan	4.17 (1.20)
Trowel	Plant pot	4.22 (1.06)
Corkscrew	Wine	4.28 (1.07)
Scoop	Ice cream	4.78 (0.55)

Note. Standard deviation in brackets.

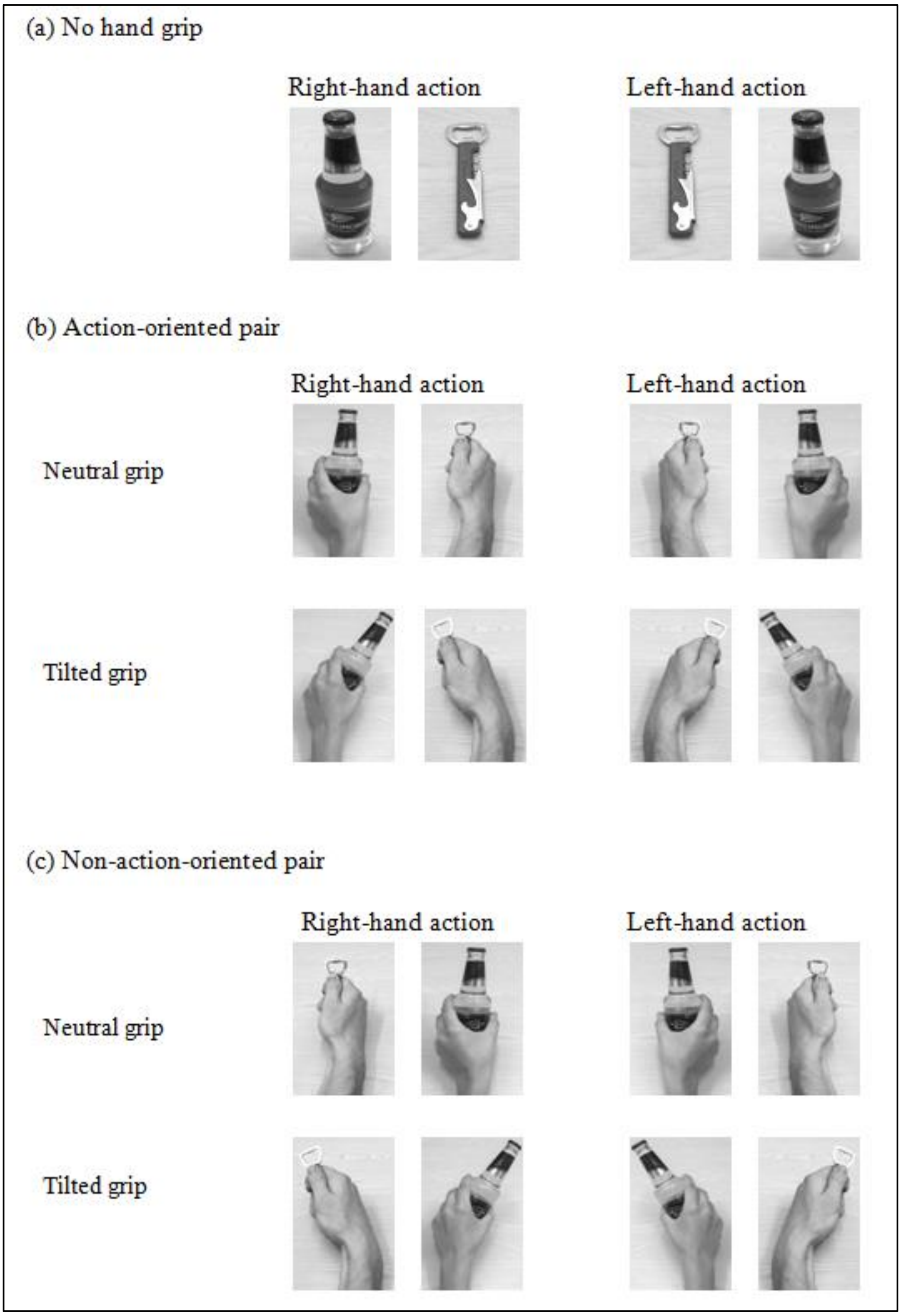


Figure 3.1. Example of experimental stimuli. Stimuli were presented with (a) no hand grip and with a hand grip (b and c). The gripped objects were (b) positioned for action and (c) not positioned for action. The hand grip posture was neutral or tilted. All pairs of objects were oriented either for right-hand actions with the tool (the bottle opener) on the right side (right panel) or for left-hand actions with the tool on the left side (left panel).

3.3.4 Design and procedure

Each participant took part in two sessions (TMS to left M1, TMS to right M1) on different days. The order of sessions was counterbalanced across participants; the order of sessions was included as covariate to ensure that differences in the session order would not affect our results. The experimental design consisted of three factors: Action relation (oriented for action, not oriented for action), Grip (no grip, neutral grip, tilted grip) and Alignment (positioned for right-hand action, positioned for left-hand action). In each session, participants completed 600 trials, 60 trials for each condition, lasting approximately 45 min. The conditions were pseudo-randomised. Each object pair was repeated four times in each condition. In addition, there were 48 catch trials in which participants performed an object detection task. Participants were instructed to press a button with the index finger contralateral to the stimulated hemisphere whenever they saw a picture of a toothpaste tube or a plug. This task was chosen to ensure that participants paid attention to the visual stimuli throughout the experiment; catch trials were not included in the analysis. Importantly, the trials of interest did not require a response, hence, any MEP responses cannot be attributed to hand movements.

Each trial began with a white central fixation presented on a black background for 3000 ms, followed by an object pair for 1000 ms. On every trial, a single TMS pulse was applied to the participants' primary left or right M1; the pulse was applied simultaneously with the offset of the object pair. MEPs were recorded simultaneously from the FDI and the ADM muscle of the contralateral hand. There was a break after every 20 trials to minimise fatigue and TMS exposure. Throughout the experiment, participants were instructed to keep both hands still and relaxed. Muscle relaxation was monitored by visual feedback of the EMG signal.

To ensure that the object pairs were highly familiar to participants', each participant was asked to evaluate each object pair for action familiarity ('How likely are these objects used together? 1-5, 1= highly unlikely, 5=highly likely') after the second session. Furthermore, participants indicated for each pair the functional role of each object within a pair ('The active object is the one that must be moved in order to perform the action (e.g., paintbrush), whereas the passive object must be held still (e.g., paint pot).'). If there was no agreement between the pre-defined functional role (active vs. passive) of each object within a pair and the individual participant's classification, we relabelled the functional role of objects accordingly. This was done to exclude possible confounding effects of culture on object use (e.g., the functional role of knife and fork is different in Europe and America). The ratings for action familiarity and object classification are presented in Table 3.1.

3.3.5 Data analysis

The MEP data were analysed off-line using a custom Matlab script (MathWorks) and IBM SPSS Statistics 21 (SPSS Inc., Chicago, IL). Trial-by-trial background EMG activity was calculated by averaging rectified EMG activity across 150 ms prior to the TMS pulse for both the FDI and ADM muscles. Any trial which exceeded 0.01 mV was removed. In addition, any trial which involved an MEP lower than 0.05 mV for either the FDI or ADM muscle was removed. In total, less than 7% of trials were removed. For each condition, the peak-to-peak amplitude was measured and averaged. The mean MEP data were examined with repeated-measures ANOVAs. Interaction effects were evaluated with paired *t*-tests ($p \leq .05$).

3.4 Results

Behavioural data revealed that the overall accuracy during the object detection task was 94% (SD = 7.33). The number of false alarms was low (1.37%); these trials were excluded from the MEP analysis.

First, we assessed whether the presence of a hand modulated M1 excitability. Next, we investigated the effects of action relation, hand alignment, and alignment on M1 excitability. Finally, we also assessed whether there was a difference in FDI and ADM muscle activation across the different conditions.

3.4.1 Effects of hand presence

To examine the effect of hand presence on M1 excitability, MEPs for action-oriented trials with no hand grip were compared with action-oriented trials with a neutral hand grip. We also tested whether there was an interaction between hand presence and muscle involvement. Contrary to our hypothesis, the presence of a hand did not modulate M1 excitability and did not differently activated FDI and ADM muscles.

The differences between no hand grip and neutral hand grip were examined with a 2 x 2 x 2 x 2 (M1 [left, right] x Muscle [FDI, ADM] x Grip [no hand, neutral grip] x Alignment [positioned for right-hand action, positioned for left-hand action]) ANOVA with session order as between-subject covariate. The mean MEPs are presented in Table 3.2. The main effect of session order did not reach significance (p = .793). There was only a reliable four-way interaction between M1, muscle, alignment and session order, F(1,16) = 4.89, p = .042, η_p^2 = .234. This four-way interaction was decomposed by analysing the data separately for the left and right M1. For the *left M1*, there were no reliable main effects or interactions.

For the *right M1*, there were reliable interactions between muscle and alignment, F(1,16) = 6.28, p = .023, η_p^2 = .282, and between muscle, alignment and session order, F(1,16) = 7.80, p = .013, η_p^2 = .328. The latter interaction was decomposed and revealed a trend towards significance for a main effect of muscle (FDI > ADM) when the right M1 was stimulated first, F(1,8) = 4.80, p = .060, η_p^2 = .375, but not when the left M1 was stimulated first (p = .382).

Table 3.2 Mean motor evoked potentials (MEPs) for the effect of hand presence as function of whether the right or the left motor cortex was stimulated first

			Session order 1		Session order 2	
Muscle	Grip	Alignment	Right motor cortex (Session 1)	Left motor cortex (Session 2)	Right motor cortex (Session 2)	Left motor cortex (Session 1)
FDI	No hand	Right-hand action	0.50 (0.22)	0.46 (0.30)	0.54 (0.44)	0.58 (0.32)
		Left-hand action	0.52 (0.30)	0.45 (0.32)	0.47 (0.36)	0.56 (0.35)
	Neutral grip	Right-hand action	0.52 (0.26)	0.40 (0.25)	0.52 (0.40)	0.56 (0.34)
		Left-hand action	0.51 (0.27)	0.45 (0.32)	0.53 (0.43)	0.59 (0.37)
ADM	No hand	Right-hand action	0.55 (0.80)	0.38 (0.32)	0.38 (0.31)	0.31 (0.17)
		Left-hand action	0.58 (0.77)	0.34 (0.31)	0.32 (0.25)	0.30 (0.22)
	Neutral grip	Right-hand action	0.55 (0.80)	0.35 (0.30)	0.35 (0.25)	0.32 (0.25)
		Left-hand action	0.57 (0.78)	0.36 (0.29)	0.39 (0.33)	0.31 (0.17)

Note. Standard deviation in brackets.

3.4.2 Effects of action relation, hand posture and hand alignment

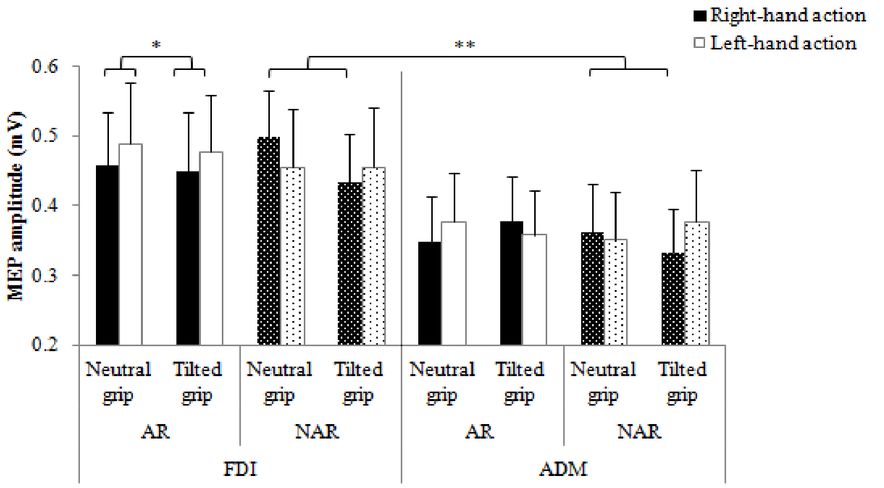
We assessed the effects of action relation, hand posture, and hand alignment on M1 excitability. We also examined whether there were muscle-specific activations. Overall, our experimental manipulations only affected right (non-dominant) M1 excitability. The mean MEPs for both motor cortices are presented in Figure 3.2.

The MEPs were entered into a 2 x 2 x 2 x 2 x 2 (M1 [left, right] x Muscle [FDI, ADM] x Action relation [oriented for action, not oriented for action] x Posture [neutral, tilted] x Alignment [positioned for right-hand action, positioned for left-hand action]) ANOVA with session order as between-subject covariate. There was no main effect of session order (p = .835). There were significant three-way interactions between M1, action relation and alignment, F(1,16) = 6.37, p = .023, η_p^2 = .285, and between M1, posture and alignment, F(1,16) = 4.97, p = .040, η_p^2 = .237. There was a trend towards significance for a four-way interaction between M1, action relation, posture, and alignment, F(1,16) = 3.95, p = .064, η_p^2 = .198, and a five-way interaction between M1, muscle, action relation, posture, and alignment, F(1,16) = 3.05, p = .080, η_p^2 = .180. To better understand these interactions, we analysed the data separately for each M1. For the *left M1*, there were no reliable main effects or interactions (Figure 3.2b).

For the *right (non-dominant) M1* (Figure 3.2a), the interaction between action relation, posture and alignment, F(1,17) = 6.88, p = .018, η_p^2 = .288, was significant. For *action-oriented objects*, there was a main effect of alignment, F(1,17) = 5.49, p = .032, η_p^2 = .244, with the MEP amplitude being larger when the tool was grasped by a left hand and presented on the left side which is associated with right M1 activation compared to right-hand actions. A reliable three-way interaction of muscle, action relation and alignment, F(1,17) = 8.46, p = .010, η_p^2 = .332, showed that the action relation and alignment interaction, F(1,17) = 3.71, p = .071, η_p^2 = .179, was observed only in the left FDI muscle. FDI MEPs were greater when the tool was on the left side and the object was on the right side compared to the opposite tool-object arrangement, *t*(17) = 2.24, p = .039.

For *non-action-oriented* trials, there was a reliable posture by alignment interaction, F(1,17) = 7.69, p = .013, η_p^2 = .311. We observed that when the tool was grasped by the right hand (and presented on the left side), MEPs for the neutral posture condition were larger compared to the tilted posture condition, *t*(17) = 2.89, p = .010. No effects were found when the tool was gripped with the left hand, *t*(17) = -.63, p = .538.

(a) Right (non-dominant) motor cortex



(b) Left (dominant) motor cortex

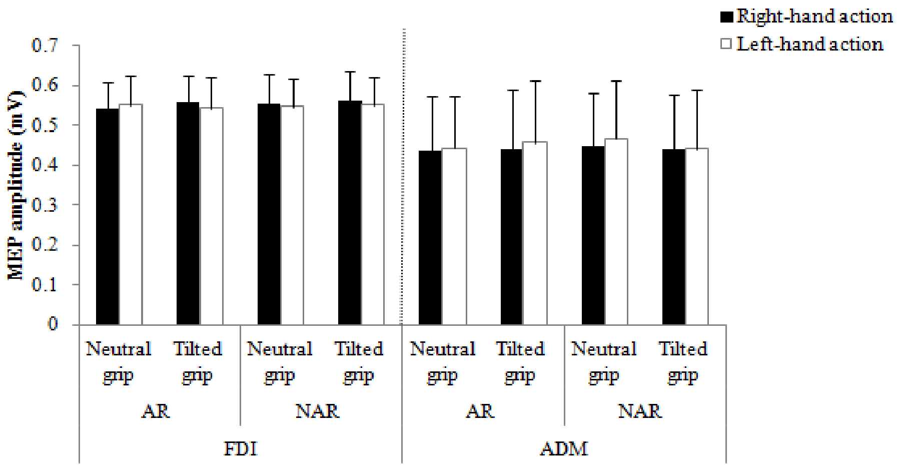


Figure 3.2. Mean peak-to-peak MEP amplitude for the right (a) and the left (b) motor cortices for all conditions. Error bars represent standard errors. Significant differences are indicated by asterisks (**p < .01, *p < .05). Abbreviations: AR = action relation; NAR = no action relation; FDI = first dorsalis interosseous; ADM = abductor digiti minini.

3.5 Discussion

This is the first study investigating whether viewing functional object pairs in different action contexts modulated left and right M1 excitability. The main results can be summarised as follows: (1) When objects were positioned for action, an increase in left hand MEP amplitude was observed for object pairs aligned for non-dominant (left-hand) compared to dominant (right-hand) actions. When objects were not positioned for action, an effect of hand posture was observed. Here objects aligned for left-hand actions elicited a lower MEP response when the hand posture was tilted compared to when it was neutral; (2) The non-dominant (right) M1 but not the dominant M1 was sensitive to our experimental manipulations; (3) In the presence of two objects positioned for actions, motor resonance reflected response to the active object rather than the passive object within the pair; (4) There was no difference in MEP amplitude between gripped objects and objects without a hand grip. (5) There was no evidence for muscle-specific activations when viewing different hand postures. The present results suggest that the right (non-dominant) M1 excitability reflects cognitive changes related to the perception and processing of paired-object affordance cues.

3.5.1 Effects of action relation, hand posture, and hand alignment on MEP response

We investigated whether the action context in which functional object pairs are presented affected M1 excitability. To do so, we presented pairs of objects oriented for action or not (hands facing each other or hands facing away), grasped with a neutral or a tilted-interactive hand posture (assuming that the latter enhances the perceived potential for action), and aligned either for left- or right-hand actions (tool grasped with the left vs. the right hand, respectively). When objects were positioned for actions, MEP amplitudes were higher when the tool was grasped with the left hand compared to when it was grasped with the right hand, irrespective of whether the hand posture was neutral or tilted. Our data fit well with the cortical lateralisation of motor dominance: Each hemisphere is specialised for contralateral action observation (Kelly et al., 2015) and movement execution (Herve, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013) but see for evidence of bilateral activation (Aziz-Zadeh et al., 2006).

The results are also in agreement with studies showing contralateral object-hand alignment effects in M1 (e.g., Drew et al., 2015; Proverbio et al., 2013; Buccino et al., 2009). Going beyond previous studies, our data first showed that when more than one object is presented in a scene, motor resonance seems to reflect alignment with the active object (the tool) rather than the passive object within correctly positioned objects for action pairs, at least in the non-dominant hemisphere. This is evident in the effect of hand alignment showing a shift from increased MEPs for left-hand than for right-hand actions when objects were action-related to increased MEP amplitude for right-handed tilted-interactive than for right-handed neutral hand postures when the objects were not action-related (in both cases the tool was always on the left side of fixation). In line with previous research, we can further confirm that the tool rather than its passive action recipient has a higher attentional weight within an object pair (for neuropsychological evidence, see Wulff et al., 2015; Wulff & Humphreys, 2015, 2013; Riddoch et al., 2003; for experimental evidence, see Xu et al., 2015; Laverick et al., 2015; McNair & Harris, 2014; Roberts & Humphreys, 2010b). Other experimental studies have also demonstrated that tools capture attention (e.g., Matheson et al., 2014; Handy et al., 2003). The present results indicate for the first time that motor excitability may depend upon contextual cues (presence of other objects) and does not seem simply derived from the affordance cues of a single object. However, further studies should evaluate M1 excitability when viewing single objects compared to object pairs to clarify the role of contextual cues on M1 excitability.

Viewing non-action-oriented objects differently affected motor resonance. In contrast to action-oriented object pairs, hand posture affected contralateral MEPs, with reduced MEP response for right-handed actions when the hand posture was tilted compared to when it was neutral. In other words, the tilted hand posture might have emphasised (or increased) the perception of the non-action relation potential of the object pair, and thus the contralateral response to the active object was stronger compared to when the hand posture was neutral.

MEPs were enhanced when the tool appeared on the left (vs. the right) side, implying that similar to the action-oriented object pair condition, the location of the tool rather than of the passive object was important, but only when there was a clear violation of the perceived action potential (as in case of tilted-interactive hand postures). This result is counterintuitive as we did not anticipate enhanced responses to tools when the objects were presented in a way that least afforded a mutual action (in our case the neutral hand posture). We assumed that tilted-interactive rather than neutral hand postures would facilitate the perception of a more direct action relationship as this posture seemed better to convey an action goal. The present results instead suggest that tilted-interactive hand postures potentially have a lower affordance due to the conflict between the position of the hands and action recipient (or at least in the case of non-action-oriented objects). In other words, when objects are not oriented for action and when objects are held with a tilted-interactive posture, the hands and the gripped objects are facing away from each other to a greater degree compared to the neutral posture (Figure 3.1), and this is more visually disruptive and less action potentiating. In contrast, neutral hand postures seem to have a higher affordance potential as the afforded bimanual action is easier to perceive. We suggest that the effect of hand posture in the non-action-oriented condition reflects the potential for action, with the affordance effect being stronger when the tool is on the left side and grasped in a neutral way. Future work is needed to further explore how the location of the tool and how the tool is grasped modulates M1 excitability. For example, exploring M1 excitability while observing single objects and tools (e.g., right-hand vs. left-hand grasp; neutral vs. tilted-interactive posture) will enable us to further disentangle the role of tools and objects within object pairs.

Contrary to our hypothesis, we did not find any evidence for a muscle-specific modulation of M1 when viewing tilted-interactive and neutral hand postures (see also review by Naish et al., 2014). We assume that the non-specific muscle activation for different hand postures is related to the coil position which was optimised for FDI. However, we observed an effect of hand alignment for action-oriented objects in the FDI but not the ADM muscle. This indicates different contributions of each of these muscles for the different hand alignments displayed to the participants. Further research is needed to clarify the relation between muscle-specific activation and hand alignment.

Overall, the present results are consistent with behavioural findings, showing improved performance for functional pairs oriented for action compared to when they are not oriented for action (e.g., McNair & Harris, 2014; Wulff & Humphreys, 2013; Humphreys et al., 2010a; Riddoch et al., 2003) as well as previous neuroimaging research demonstrating different pre-motor and motor cortices activity for action-oriented and non-action-oriented object pairs (Wulff et al., 2014). In line with Bestmann and Krakauer (2015), we assume that the observed MEPs reflect action preparation processes in motor-related areas which feed into M1 (see also, Cisek & Kalaska, 2010; Aziz-Zadeh et al., 2002). Thus, we suggest that M1 represents cognitive changes based on the perception and processing of paired objects.

3.5.2 Differences between left and right M1 excitability

To our surprise, we observed a different pattern of excitability for the left and the right M1. More specifically, our paradigm revealed that only the non-dominant (right) M1 was influenced by the experimental manipulations of action relation, hand alignment and hand grip. Based on this result, it is unlikely that the response hand (contralateral to TMS stimulation) interfered with motor preparation. If this would be the case, we would expect an effect of hand alignment (see above) in both motor cortices. This was not the case in the present study.

It is possible that this hemispheric asymmetry was due to differences in processing uni- vs. bimanual actions; note that all our stimuli depicted bimanual actions. This is supported by recent research showing that the recruitment of the left or the right M1 depends upon the type of movement. For example, the observation of bi- in contrast to unimanual actions led to stronger non-dominant M1 activity (Heitger et al., 2012). Moreover, virtual lesions, elicited by TMS over the non-dominant pre-motor cortex, disrupted bi- but not unimanual movements (van den Berg et al., 2010).

A second potential explanation for the observed motor excitability asymmetry is the motor familiarity with the observed hand-object interaction. Greater excitability of the non-dominant M1 compared to the dominant M1 has been previously reported using the TMS stimulus-response curve technique (Daligadu, Murphy, Brown, Rae, & Yielder, 2013; Semmler & Nordstrom, 1998). The authors argued that this asymmetry may be related to differences in motor skills, and thus hand use. In everyday life, we commonly observe actions performed with the left and the right hand. However, we are less familiar with using the left hand when interacting with the active object within a pair (e.g., right-handers will typically hold the bottle in their right (but not left) hand when pouring). Similarly, Cross et al. (2012) showed that unfamiliar (robot-like) compared to familiar (human-like) actions enhanced right pre-motor cortex activity, though opposite results have been also reported (Plata Bello, Modrono, Marcano, & Gonzalez-Mora, 2013; Cross, Hamilton, Kraemer, Kelley, & Grafton, 2009). Other studies have shown that the less “automated” an action is (e.g., using the left hand), the more widespread motor-related activities were evident (e.g., Schluter et al., 2001; Jenkins et al., 1994). This effect was specifically observed in the SMA, where unfamiliar but plausible functional object pairs elicited more responses than familiar and common action pairs (Hoeren et al., 2013). It is interesting to note that behavioural studies typically report a performance benefit for objects aligned with the preferred hand compared to not aligned objects (e.g., Vankov & Kokinov, 2013; Yoon et al., 2010; Humphreys et al., 2010a), while neuroimaging evidence has revealed an inverse effectiveness pattern between motor response and the degree of action familiarity. Therefore, it is possible that the level of motor excitability reflects the degree of motor familiarity, with greater excitability for the non-dominant hemisphere when the unfamiliar hand is used or observed.

A third explanation is that the dominant (left) hemisphere in right-handed participants codes both ipsilateral and contralateral movements, while the non-dominant hemisphere is only activated by contralateral movements (e.g., Hlustik, Solodkin, Gullapalli, Noll, & Small, 2002; Schluter et al., 2001; Kim et al., 1993). Recall that in all stimuli used the objects were gripped by both the right and the left hand. Accordingly, it could be that the dominant hemisphere is equally sensitive to active and passive hand grips (i.e., bimanual actions) regardless of familiarity. In line with this idea are the findings of greater hand representations (e.g., Volkmann, Schnitzler, Witte, & Freund, 1998; Wassermann, McShane, Hallett, & Cohen, 1992) and lower motor threshold (e.g., Macdonell et al., 1991) in the dominant M1 compared to the non-dominant M1. Moreover, it has been shown that the left M1 in right-handers is larger than the right M1 (Amunts et al., 1996).

We can exclude the possibility that the observed right M1 excitability was due to increased TMS intensity compared to the left M1 (stimulus intensity was only marginal higher for the right M1 compared to the left M1). However, as it can be seen in Figure 2, the MEPs for the right M1 were numerically smaller (M = 0.41) compared to the left M1 (M = 0.50). Thus, it could be that the smaller MEPs in the right M1 enabled us to observe differences between conditions. A future study should explore the effects of TMS stimulus intensities on left and right M1 excitability.

3.5.3 Effects of hand presence on MEP response

In contrast to previous studies, we did not find an effect of hand presence on M1 excitability. Enhanced MEP response for grasping movements towards objects compared to objects presented in isolation has been previously demonstrated (e.g., Fadiga et al., 1995). The reason for this contrasting finding may be due to nature of the stimuli. We presented static pictures of objects with or without a hand grip, while participants observed dynamic grasping actions and static observation of objects alone in Fadiga et al.'s study (1995). It is also possible that our stimuli depicted with and without a hand grip had a similar level of affordance; the two conditions were identical with the exception that no or one hand was depicted. We suggest that objects with identical visual properties have the same action potential, and thus elicit a similar affordance response. This assumption is supported by Kumar et al. (2012) who also showed that there was no difference in EEG response between single objects alone or congruently gripped objects in frontal motor regions.

3.6 Conclusion

This chapter aimed to further explore the role of M1 in paired-object affordance. We first demonstrated that motor excitability is influenced by contextual information (presence of other objects), with the perceived affordance modulating M1 excitability. More specifically, right (non-dominant) M1 excitability was sensitive to action relation, hand posture and hand alignment, with greater MEP responses when the tool was gripped by the non-dominant hand and when the objects were oriented for action. The data suggest that M1 likely reflects cognitive changes based on the perception of paired objects.

CHAPTER 4: VISUAL RESPONSES TO ACTION BETWEEN UNFAMILIAR OBJECT PAIRS MODULATE EXTINCTION[1]

4.1 Abstract

The next two chapters are concerned with the effects of paired-object affordance on visual extinction by manipulating visual-based affordance cues (manipulating familiarity with the object pair; Chapter 4) and motor-based affordance cues (manipulating graspability of the stimuli; Chapter 5). In both chapters, object identification performance was used as an index of attentional allocation, and thus recovery from visual extinction. Previous studies show that positioning familiar pairs of objects for action ameliorates visual extinction in neuropsychological patients (Riddoch et al., 2003). This effect is stronger when objects are viewed from a 1PP and are placed in locations congruent with the patient's premorbid handedness (Humphreys et al., 2010a), consistent with it being modulated by a motor response to the stimuli (see also Chapters 2 and 3). There is also some evidence that extinction can be reduced with unfamiliar object pairs positioned for action (Riddoch et al., 2006), but the effects of reference frame and hand-object congruence have not been examined with such items. This was investigated in the present chapter. There was greater recovery from extinction when objects were action-related compared to when they were not, in line with previous studies. In addition, patients benefited more when they saw action-related pairs from a 3PP than a 1PP. Interestingly, on trials where extinction occurred, there was a bias reporting the active object on the extinguished side – a reversal of the standard pattern of

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[1] Chapter 4 is an adapted version of Wulff, M. & Humphreys, G. W. (2013). Visual responses to action between unfamiliar object pairs modulate extinction. *Neuropsychologia,* 51, 622-632.
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extinction – but only when objects were seen from a 1PP. The data show that several factors contribute to the effects of action relations on attention, dependent upon the familiarity of the object pairs and the reference frame that stimuli have been seen in.

4.2 Introduction

Visual extinction, a neuropsychological disorder of spatial attention, can disrupt the ability of patients to report items in complex, multi-stimulus displays. Extinction is commonly found after damage to the (right) posterior parietal cortex and is characterised by the failure to detect a contralesional stimulus accompanied simultaneously by an ipsilesional stimulus (e.g., Chechlacz, Rotshtein, Demeyere, Bickerton, & Humphreys, 2014; Chechlacz et al., 2013; Driver & Vuilleumier, 2001; Karnath, 1988). Several behavioural studies have demonstrated that, despite the lack of report, there is evidence that contralesional stimuli are processed. Notably, the relations between the contra- and ipsilesional stimuli affect extinction, with extinction reduced when these stimuli group together. There is now evidence for a wide variety of grouping cues being effective in reducing extinction. Extinction can be modulated by grouping on the basis of Gestalt principles such as similarity and contrast polarity (e.g., Gilchrist, Humphreys, & Riddoch, 1996), by stored knowledge about familiar shapes (Ward, Goodrich, & Driver, 1994) and by lexical identity (Kumada & Humphreys, 2001).

Patients are also able to overcome their pathological bias to favour the ipsilesional stimulus when the stimulus itself affords an action. For example, di Pellegrino et al. (2005) demonstrated that patients showed less left visual extinction when the handle of a contralesional cup afforded a left-hand rather than a right-hand grasp (cf. Gibson's affordance concept, 1979). They proposed that the observation of a handle results in an automatic activation of motor programs to reach and grasp the object that, in turn, biases visual selection and stimulus detection. Interestingly, affordance effects in extinction patients have been reported not only for single objects (e.g., di Pellegrino et al., 2005) but there is also evidence for effects of action relation between objects. For example, Riddoch et al. (2003) first showed that positioning objects for action reduced extinction in patients with parietal lesions. Riddoch et al. presented two objects (e.g., a paint pot and a paintbrush) either positioned to interact with each other (the paintbrush about to dip into the paint pot) or not (the paintbrush facing away from the paint pot). Extinction was less severe when objects appeared in the correct positions for action, while there was no recovery from extinction when the same objects were positioned incorrectly for action. Riddoch et al. proposed that familiar objects co-positioned for action were grouped together as a unitary configuration. The objects could then be selected as a single perpetual unit even when one fell in the contralesional field and would be otherwise subject to extinction. Consistent with this argument for configural coding of action-related stimuli, Riddoch et al. (2011) reported that the effects of action relations were disrupted if manipulations were introduced to disturb configural coding, such as inverting the stimuli or alternating their relative sizes. In addition, the effects were not semantic in nature, because no benefits on extinction were found with pairs of objects that were associatively related (e.g., tin and can) rather than action-related (Riddoch et al., 2003).

One other interesting result reported by Riddoch et al. (2003) concerned performance on extinction trials, when patients only reported one of the two object presented. Standardly patients are biased to report the ipsilesional stimulus on these trials. Riddoch et al. found an exception to this, when objects were positioned to interact together. With these stimuli Riddoch et al. found a preferential report of the active member of the pair (the object that would be used on the other item), irrespective of whether it fell in the contra- or ipsilesional field. Thus, on trials where the active object fell in the contralesional field, patients reported the contralesional stimulus more often than the ipsilesional stimulus – that is; there was a reversal of the standard spatial extinction effect. Riddoch et al. suggested that patients could implicitly code the presence of an interacting pair of objects and with some stimuli, attention was cued first to the active member of the pair. This led to this item being preferentially reported on trials where extinction occurred. Converging evidence for attention being drawn to the active member of an interacting pair comes from Roberts and Humphreys (2010b) who used a measure of “prior entry” on temporal order judgements.

These results with interacting objects are of considerable interest since they indicate that visual attention is sensitive not only to low-level perceptual regularities (e.g., collinearity between edges) but also to higher-level regularities based on the co-occurrence of objects in action (see Riddoch et al., 2011). However, the underlying factors and processing mechanisms that determine these effects remain poorly understood. For example, are the effects based on the perceptual familiarity of object pairs, on perceptual coding of action or on associated motor responses that may be evoked by pairs of interacting objects?

There is evidence that the perceptual familiarity of the object pairs themselves is not critical. Riddoch et al. (2006) used pairs of objects with a low frequency of co-occurrence but which were positioned to interact together. They again found recovery from extinction. The presence of the action relation alone seemed important here. Evidence for perceptual sensitivity to these action relations comes from Roberts and Humphreys (2010a), who examined brain activity when participants viewed objects co-located or not co-located for action. These investigators found enhanced activity in visual cortical regions (e.g., the LOC and the FFG) when objects were co-located for action compared with when they were not co-located for action. The results are consistent with action-related objects yielding an enhanced perceptual response.

On the other hand, there is also evidence for motor-related responses in relation to action-based properties of images. For instance, Kumar et al. (2012) reported early activity over motor cortex (N1 component) when participants viewed images of objects being grasped correctly relative to when they were grasped incorrectly for action. Neuropsychological evidence comes from Humphreys et al. (2010a) who presented familiar pairs of objects to patients showing visual extinction. The objects were either positioned correctly for action or reflected so that they were positioned incorrectly. In addition, the active member of the pair could be aligned with the patient's premorbidly dominant hand or not, and the stimuli were depicted either from a 1PP (in the patient's own reference frame) or from a 3PP (as if seen from the opposite side of a table). Humphreys et al. found that recovery from extinction was stronger when the objects were held in hands congruent with the premorbidly dominant hand for the patient and this effect was enhanced when the objects were seen from a 1PP compared to a 3PP. The effect of hand alignment suggests that action-related objects may evoke a stronger motor response than action-unrelated objects. This response may be particularly potent when the stimuli are presented in a 1PP, consistent with vasomotor coupling driving attention to action-related objects (cf. Humphreys et al., 2010b; see also Valyear, Gallivan, McLean, & Culham, 2012, for fMRI evidence).

In the present chapter we extended this prior result by examining whether these visuomotor responses are sensitive only to the implied action, when objects are co-located for action, or also to the visual familiarity of the object pairs. To do this, we replicated the procedure of Humphreys et al. (2010a), but this time used pairs of objects not normally used together and so not familiar as a pair. Is the mere presence of an action, between objects paired for action, sufficient to alleviate the contralesional attentional deficit in extinction patients, even if the objects are not usually used together? Based on a previous study using unfamiliar object pairs (Riddoch et al., 2006), we expected that there would be recovery from extinction when objects are oriented for action compared to when they are not oriented for action. More importantly, we asked if recovery from extinction occurred, is it visual- or motor-related (e.g., is there a visual-based affordance effect of the reference frame or a motor-based affordance effect determined by whether the objects align with the patient's premorbidly dominant hand)? We assessed whether these factors modulated the ability of the patients to report both objects, on a two-object trial, and also whether they influenced attention to objects within a pair, on extinction trials (cf. Riddoch et al., 2003). We expected a preferential report of the active member of the pair. To maximise the action effects, we showed objects grasped by a hand that was congruent with the action normally performed with the object, extending Gibson's affordance concept (1979). Previous studies have shown that the presence of the hand grasp maximises affordance-based responses to objects (e.g., Kumar et al., 2012).

4.3 Methods

4.3.1 Patients

Ten brain-damaged patients with visual extinction, comprising 2 females and 8 males from 39 to 78 years of age (M = 67.70; SD = 11.63), were recruited from the volunteer panel at the School of Psychology, University of Birmingham. Five patients (JB, MC, MP, TH, and TM) had right unilateral lesions, three (DT, PH, and RH) had left unilateral lesions, and two (PF, and PM) had bilateral lesions (clinical details are given in Table 4.1, and lesion reconstructions are shown in Figure 4.1). Seven patients showed left visual extinction, and the remaining (DT, PH, and RH) showed right visual extinction. Since the terms “ipsilesional” and “contralesional” are misleading in the case of bilateral lesions, we instead use the terms “non-extinguished” and “extinguished”, respectively. Patients did not have visual field defects on visual confrontation testing. None of those patients suffered from optic ataxia. Four patients (JB, PF, PM, and RH) had a clinically defined problem in either gesture recognition (1 patient), gesture production (2 patients) or imitation (2 patients) on the BCoS Cognitive Screen (Humphreys, Bickerton, Samson, & Riddoch, 2012). However, the extinction data for these patients were not obviously different from the results of the other patients. All except four (JB, MP, RH, and TH) were right-handed as tested by the Edinburgh Handedness Inventory (Oldfield, 1971). All reported normal or corrected-to-normal vision. Informed consent was obtained from all patients and the study was approved by a national NHS research ethics committee. The experiment was conducted over a period from November 2009 to March 2012. Each patient’s performance was relatively stable across this period.

Table 4.1 Demographic and clinical data of the patients

Patient	Sex / age / handedness	Main lesion site	Major clinical symptoms	Aetiology	Time since lesion (years)
DT	M / 70 / R	Left lingual and fusiform gyrus	Right extinction	Stroke	5
JB	F / 76 / L	Right parietal (angular and supramarginal gyri, inferior parietal lobe), temporal (inferior, middle and superior temporal gyri) and frontal (inferior and middle frontal gyri) cortex; left inferior occipital, lingual and parahippocampal gyrus	Left extinction; neglect in reading and writing	Stroke	13
MC	M / 78 / R	Right occipito-parieto-temporal cortex extending to the inferior frontal gyrus	Left neglect; left extinction	Stroke	5
MP	M / 64 / L	Right fronto-temporal-parietal regions (inferior and middle frontal gyrus, middle and superior temporal gyrus, supramarginal gyrus and inferior parietal lobe)	Left neglect and extinction; mild left hemiplegia; dyscalculia	Aneurism	20
PF	F / 63 / R	Bilateral lesions to the posterior parietal cortices (inferior and superior parietal lobe, the intraparietal sulcus and angular gyrus) extending more inferiorly in the left hemisphere	Left extinction; dysgraphia	Stroke	11
PH	M / 39 / R	Left medial and superior temporal lobe, left inferior and middle frontal gyri	Right extinction; right hemiplegia; aphasia	Stroke	12
PM	M / 70 / R	Bilateral parietal cortices	Left extinction	Stroke	8
RH	M / 78 / L	Left inferior parietal (supramarginal and angular gyrus) and superior temporal gyrus	Right extinction; neglect in reading	Stroke	13
TH	M / 64 / L	Right parietal cortex	Left extinction	Stroke	4
TM	M / 75 / R	Right inferior parietal cortex (angular gyrus and inferior parietal lobe), superior temporal and inferior frontal cortex	Left neglect; left extinction; dense left hemiplegia	Stroke	11

Note. M = male; F = female; R = right; L = left.

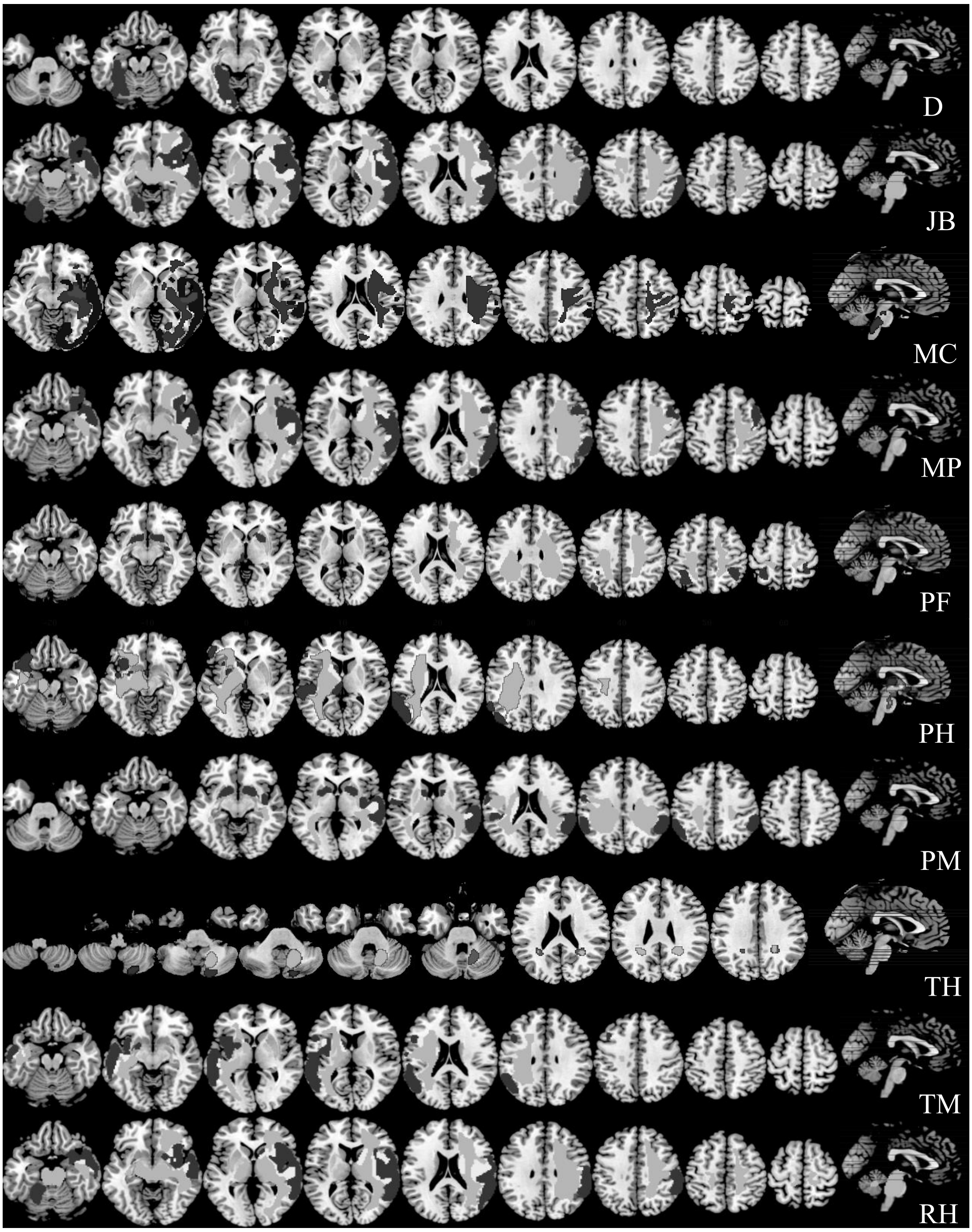

Figure 4.1. Anatomical location of patients' lesions. The figure depicts T1 structural scans (taken at 3T, with a 1-mm isotropic resolution). Grey matter (dark grey) and white matter (light areas) lesions for each patient were identified using voxel-based morphometry (VBM) in SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/) by comparing patients relative to healthy controls (N=140) aged 40 years or older with no history of brain lesions. The lesions were then overlaid on a standard multi-slice template in MRIcron (http://www.sph.sc.edu/comd/rorden/mricron/). The analyses are based on one-sample *t*-tests with three covariates: healthy grey-white matter versus patient grey-white matter, age, and sex, with a family-wise error correction (FWE) of p < .05) and a minimum cluster size of 100 voxels.

4.3.2 Apparatus and stimuli

Thirty-two coloured photographs of common objects the same as those in Humphreys et al. (2010a) were used. Each item was depicted grasped by a hand and held above a table, photographed from a 1PP and from a 3PP. The individual items for each perspective were combined into 16 object pairs that were not commonly used together (e.g., paint pot and bottle opener; see Figure 4.2a and Figure 4.2b for the 1PP and the 3PP, respectively). All object pairs are listed in Appendix 1. Each object pair was presented simultaneously, one stimulus to the right and the other stimulus to the left side of fixation. The stimuli appeared on a black background.

Following the classification of active and passive objects by Riddoch et al. (2003) each object pair was divided into: (i) an active object (e.g., a bottle opener) grasped by a right hand and a passive object (e.g., the paint pot) held by a left hand, or (ii) an active object grasped by a left hand and a passive object held by a right hand (see Appendix 1). Note that these conditions were evaluated relative to the patient’s own handedness, e.g., for a right-handed person represents (i) a “congruent” grasp condition and (ii) an “incongruent” grasp condition. These two conditions were depicted with the items arranged either to afford a mutual action or not (referred to as correct action relation or incorrect action relation, respectively). This resulted in four two-item conditions [action-relation (correct/incorrect) x grasp (congruent/incongruent)] for each perspective.

One-item trials were intermingled with the two-item trials. Here, an item in the left or right hemifield was paired with a blank table on the other side of fixation (to maintain approximate levels of visual stimulation), and it was presented at the same location and for the same duration as it appeared on bilateral trials.

The stimuli were presented with E-prime software (Version 2.1; Psychology Software Tools, 2006). Visual stimuli were displayed on a 19-inch monitor at a viewing distance of approximately 50 cm. The monitor provided a frame refresh rate of 75 Hz with a spatial resolution of 1024 x 768 pixels. The stimuli subtended 10.29° x 8.56° of visual angle and were located 0.86° either to the left or right side of central fixation.

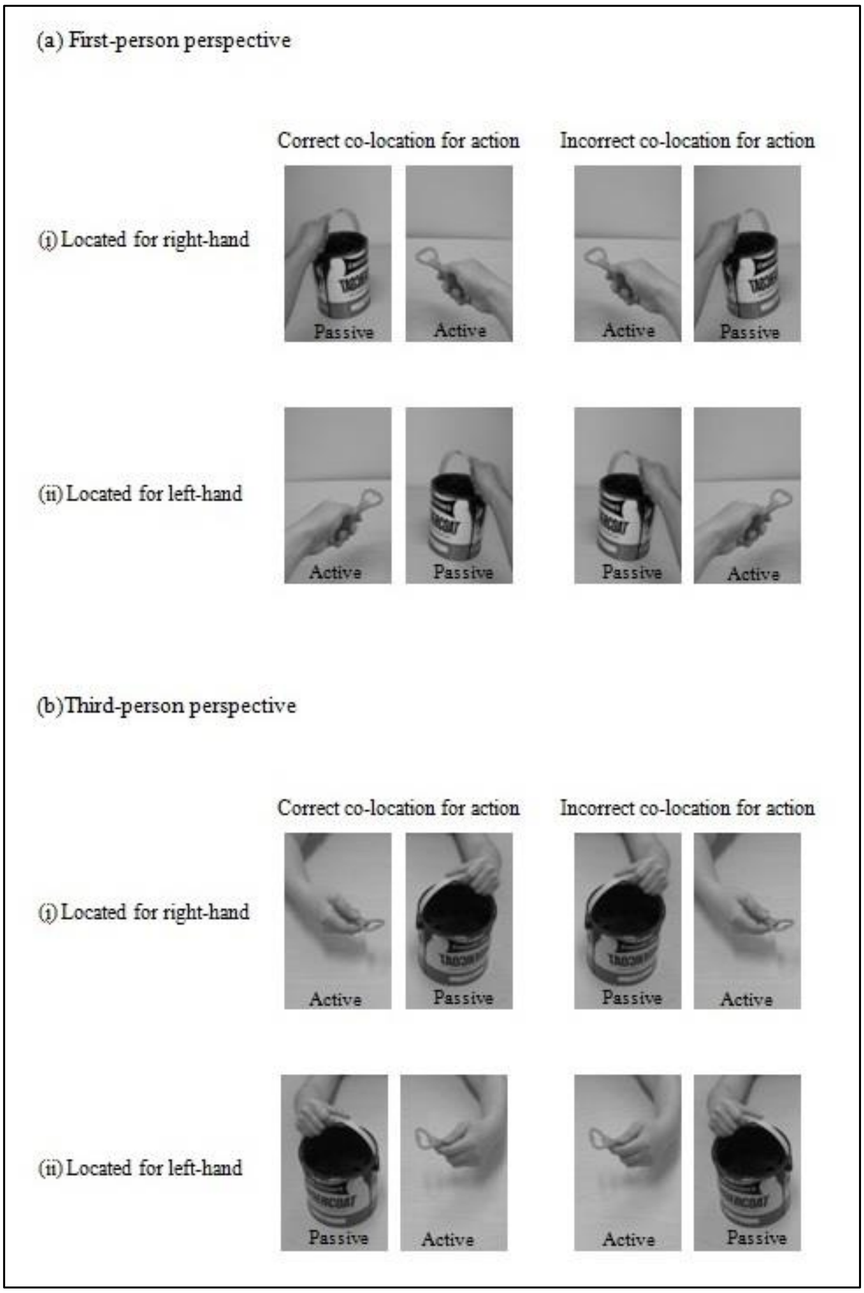

Figure 4.2. Examples of two-item stimuli presented either from a first-person perspective (a) or from a third-person perspective (b). The stimuli are shown in the correct co-locations for action (left panels) and the incorrect co-locations for action (right panels). The active object (the bottle opener) is grasped either by the right hand (upper panels) or the left hand (lower panels).

4.3.3 Design and procedure

A similar design to Humphreys et al. (2010a) was used. The experiment consisted of two perspective conditions (1PP vs. 3PP) which were administered to each patient in an ABBA order. The order of the perspectives was counterbalanced across patients. Each perspective condition consisted of four bilateral conditions [action relation (correct/incorrect) × grasp (congruent/incongruent)] and four unilateral conditions [stimulus type (object/tool) x side of stimulus (non-extinguished/extinguished)].

There were 768 trials, 384 for each perspective, and the stimuli were presented in 24 blocks of 32 trials; 48 trials for each condition. Each patient participated in six sessions which were at least one week apart. Each session consisted of four blocks. Across the four blocks the conditions were fully randomised and the order of the blocks was counterbalanced across patients. The items were repeated in different conditions across the four blocks.

Patients were tested individually in a quiet room. Before each session, pictures of the stimuli were presented individually on a monitor to each patient to ensure that the patients could recognise and correctly identify the items. Additionally, patients were given at least two training blocks of 16 trials to ensure adequate performance with the task; these results were not included in the data analysis. The stimuli on practice trials were different from those employed in the experimental trials to avoid carry-over effects. Stimulus exposure time was adjusted to ensure that each patient achieved a performance level of roughly 70-90% correct for single items presented in the extinguished hemifield (Table 4.2). Four age-matched controls tested on the fastest exposure duration as for patient PF (150 ms) performed at ceiling.

Patients had to identify and name the item(s) on each trial by verbal report. Responses were manually recorded by the experimenter, and after that the next trial was initiated. As is typical in studies of extinction, our emphasis was on the accuracy rather than the speed of response. Note that reaction time (RT) cannot be recorded to extinguished stimuli[1]. The patients were instructed to maintain fixation throughout the experiment and to respond as accurately as possible. Fixation was monitored by the experimenter. Each trial began with a white central fixation cross presented on a black background for 2000 ms. This was replaced by a red fixation cross for 500 ms to inform patients that the stimulus was about to appear. Next, a single object or an object pair was presented. For patient PF only a 100 ms mask followed the object(s) in order to maintain the same level of task difficulty across patients.

Table 4.2 Stimulus exposure times for the first-person and the third-person perspective

Patient	First-person perspective	Third-person perspective
DT	500 ms	500 ms
JB	M=517 ms (Session 1: 500 ms, Session 2: 500 ms, Session 3: 550 ms)	500 ms
MC	1000 ms	M= 433ms (Session 1: 500 ms, Session 2: 400 ms, Session 3: 400 ms)
MP	5000 ms	M=4333ms (Session 1: 5000 ms, Session 2: 4000 ms, Session 3: 4000 ms)
PF	150 ms	150 ms
PH	200 ms	M=183 ms (Session 1: 150 ms, Session 2: 200 ms, Session 3: 200 ms)
PM	M=325 ms (Session 1: 300 ms, Session 2: 325 ms, Session 3: 350 ms)	500 ms
RH	500 ms	500 ms
TH	200 ms	200 ms
TM	M=1125 ms (Session 1: 1000 ms, Session 2: 1375 ms, Session 3: 1000 ms)	1500 ms

Note. M = Mean.

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[1] We acknowledge that it would have been interesting to record RTs.

4.4 Results

The analyses were conducted across both perspective conditions. First, we assessed whether there was a spatial extinction effect. Next, we investigated the effects of action relation on two-item report. Finally, we assessed whether there was a difference in reporting the active and passive member within each object pair on two-item trials, when only one item was correctly reported (referred to as error trials).

For statistical analysis of the accuracy data, a repeated-measures ANOVA was adopted using SPSS for windows 19.0 software (SPSS Inc., Chicago, IL). Significant differences between conditions were further assessed with paired *t*-tests. The significance level was set at $p \leq .05$.

4.4.1 The presence of extinction

Extinction was diagnosed by comparing performance on one-item trials with performance on two-item trials. Extinction was present if the patient's identification performance was better on one-item than on two-item trials. The two-item trials were taken from the unrelated condition (i.e., incorrectly positioned object pairs) only, as this provided a baseline for extinction (cf. Humphreys et al., 2010a; see also Rees et al., 2000).

The accuracy data from one-item and incorrectly positioned two-item trials were entered into a four-factor mixed design ANOVA, with the within-subject factors being perspective (1PP vs. 3PP), number of objects (one-item trials vs. incorrectly positioned two-item trials) and side of item being reported (non-extinguished vs. extinguished); patient was treated as a between-subject factor. Each testing session was entered as a participant nested within the patient factor.

Performance on one-item trials was generally better than on two-item trials, confirming that visual extinction was present. The main effect of perspective was significant, F(1,20) = 4.60, $p = .045$. The main effects of number of objects, F(1,20) = 684.55, $p < .001$, and patient, F(9,20) = 5.08, $p < .01$, were also significant. Identification performance was better on one-item than on incorrectly positioned two-item trials; it was better for 3PP than for 1PP stimuli, and overall performance varied across patients. The interaction between perspective and number of objects reached significance, F(1,20) = 14.45, $p < .01$ (Figure 4.3). The extinction effect was larger in the 1PP compared to the 3PP, though it was reliable for both, *t*(29) = 13.62, *t*(29) = 9.22, both $p < .001$, respectively (the advantage for one- over two-item trials was 41% for the 1PP and 33% for the 3PP). There were also interactions between the number of objects and patient, F(9,20) = 10.77, $p < .001$, and between perspective, number of objects and patient, F (9,20) = 4.64, $p < .01$. Although the extinction effect was apparent in all patients, the magnitude of the effect varied across patients and perspectives. The variations across patients are shown in Figure 4.4. No other main effects or interactions were significant ($p > .05$).

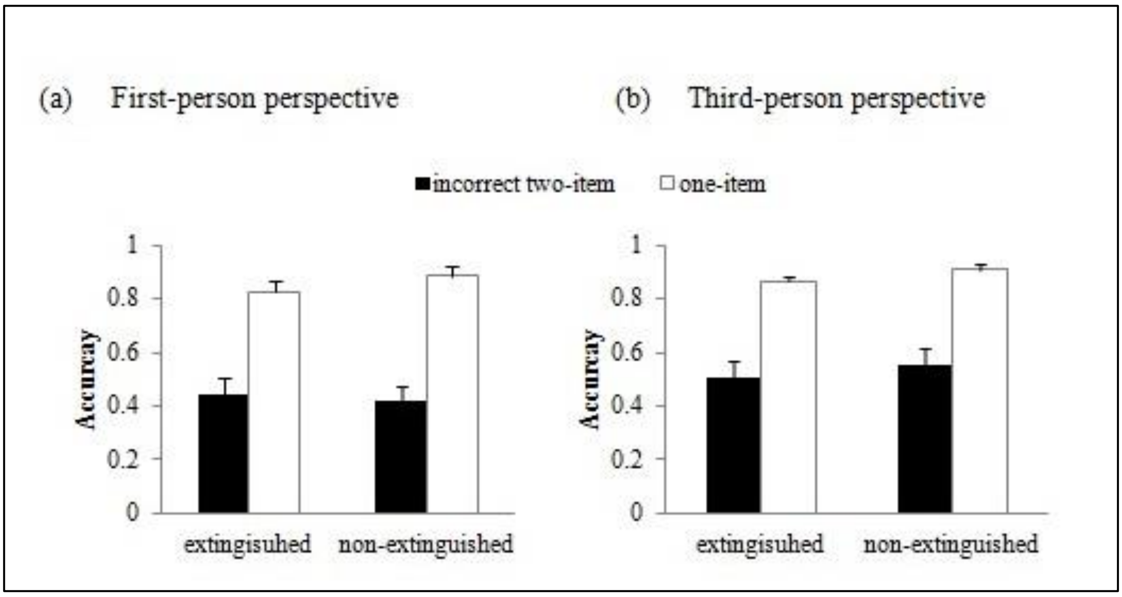


Figure 4.3. The relations between number of objects (one- vs. unrelated two-items) and side (non-extinguished vs. extinguished) as function of the perspective (mean accuracies). Bars indicate standard errors.

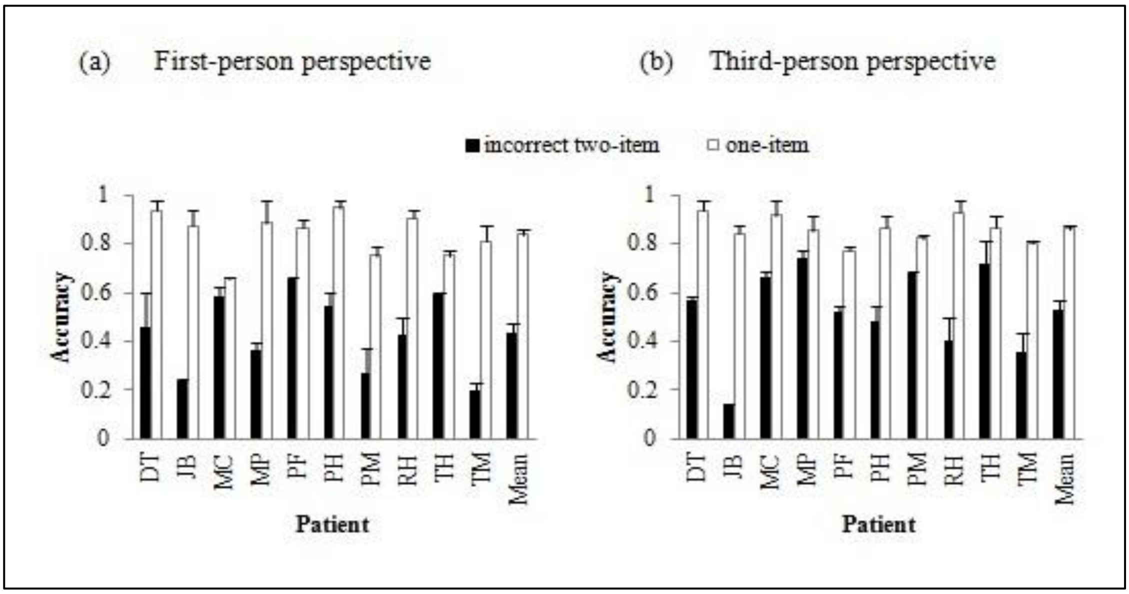


Figure 4.4. Mean patient accuracies (with standard errors) on one-item and incorrect (unrelated) two-item trials for the first-person perspective (a) and for the third-person perspective (b).

4.4.2 Effects of action relation on two-item report

We examined whether there was recovery from extinction when objects were oriented for action compared to when they were not oriented for action and whether this effect was modulated by which hand is holding the objects and in which perspective the objects were presented in. The accuracy data for two-item trials were also analysed in a four-factor mixed design ANOVA, with the within-subject factors being perspective (1PP vs. 3PP), co-location for action (correct vs. incorrect) and grasp (congruent vs. incongruent); patient was treated as a between-subjects factor. As before, each session was entered as a participant nested within the patient factor.

There was a main effect of perspective, F(1,20) = 8.11, p < .05. Accuracy was higher when object pairs were presented from a 3PP relative to a 1PP. There was a main effect of co-location for action, F(1,20) = 98.98, p < .001 (see Figure 4.5), with better performance when objects were arranged in the correct co-locations for action compared to when they were not correctly located for action. There was a main effect of patient, F(9,20) = 9.41, p < .001, indicating that performance varied across patients. There was a significant interaction between co-location for action and patient, F(9,20) = 8.94, p < .001. The effect of action relation was apparent in all patients tested, though the magnitude varied across the patients (see Figure 4.6). The interaction between co-location for action and grasp was also reliable, F(1,20) = 10.32, p < .01. The effect of action relation was greater in the incongruent than in congruent grasp conditions, *t*(29) = 5.73, p< .001, *t*(29) = 3.79, p< .01, respectively. The three-way interaction (co-location for action x grasp x patient) also reached significance, F(9,20) = 3.27, p < .05. Thus, patients differed in the degree to which they showed a greater effect of action relation with incongruent relative to congruent hand assignments. In addition, the four-way interaction (perspective x co-location for action x grasp x patient) was reliable, F(9,20) = 2.92, p < .05, indicating that the effect of action relation varied according to the grasp and perspective as noted above, but the magnitude of this effect varied across patients (Figure 4.6).

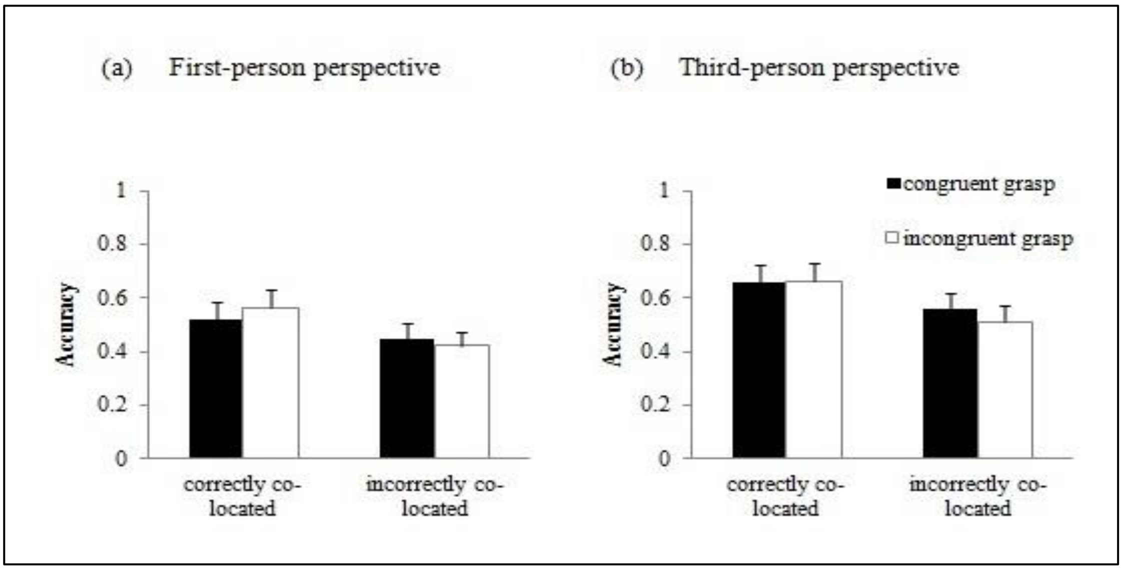


Figure 4.5. Mean accuracy of performance on correctly and incorrectly positioned two-item trials for first-person perspective (a) and third-person perspective (b), with error bars indicating standard error.

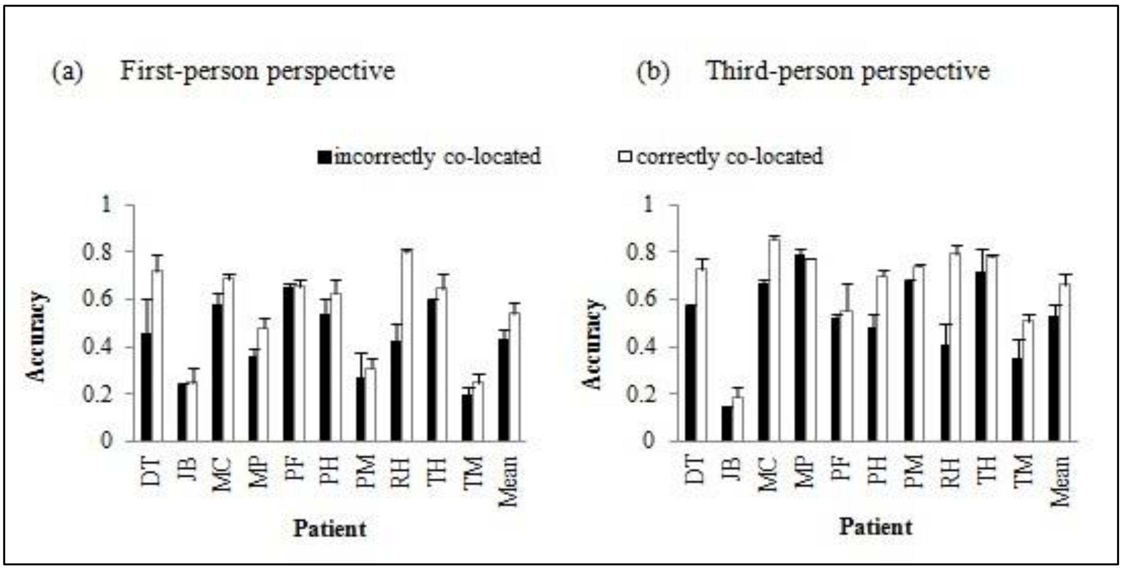


Figure 4.6. Effects of action relation on two-item trials for first-person perspective (a) and third-person perspective (b), with error bars indicating standard error.

4.4.3 Effects of action relation on identification errors on two-item trials

The error data from two-item trials when only one item of an object pair was correctly reported were entered into a log-linear analysis, with the factors being perspective (1PP vs. 3PP), co-location for action (correct vs. incorrect), side of active partner (active partner either on the non-extinguished or on the extinguished side) and side of reported item (either on the non-extinguished or on the extinguished side).

The final model showed that the highest-order interaction (the perspective x co-location for action x side of active partner x side of reported item interaction) was significant, $\chi^2(1) = 10.88$, $p < .001$. The likelihood ratio of this model was, $\chi^2(0) = 0$, $p = 1$. Performance was then analysed separately as a function of whether the object pair was correctly or incorrectly positioned for action, with the factors being perspective, side of active partner and side of reported item. When the object pair was correctly positioned for action, there was a reliable three-way interaction between perspective, side of active partner and side of reported item, $\chi^2(1) = 112.54$, $p < .001$, and the likelihood ratio of the model was, $\chi^2(0) = 0$, $p = 1$. When the object pair was incorrectly positioned for action, there was again a three-way interaction between perspective, side of active partner and side of reported item, $\chi^2(1) = 47.44$, $p < .001$.

To break down these two three-way interactions, separate log-linear analyses were conducted across performance where, for the correct and incorrect co-locations conditions, the active partner appeared on the non-extinguished or extinguished side. The factors were perspective and side of reported item. The results are presented in Figure 4.7 and Figure 4.8. There were four analyses.

1. C*orrect co-location for action condition when the active partner is on the non-extinguished side*. There was a final model in which there were only significant main

effects of perspective, $\chi^2(1) = 4.38$, $p < .05$, and side of reported item, $\chi^2(1) = 63.94$, $p < .001$. The likelihood ratio of the model was, $\chi^2(1) = 3.75$, $p = .053$. There was better performance in reporting non-extinguished (active) compared with extinguished (passive) items and there were more single item reports when the stimuli appeared in the 1PP compared to the 3PP.

2. *Correct co-location for action condition when the active partner is on the extinguished side*. The final model showed a reliable interaction between perspective and side of reported item, $\chi^2(1) = 192.20$, $p < .001$, and the likelihood ratio of the model was, $\chi^2(0) = 0$, $p = 1$. Patients reported more non-extinguished than extinguished items, but this held only for the third-person perspective. In contrast, there were more reports of the extinguished (active) than the non-extinguished (passive) item when the stimuli were seen from a 1PP.
3. *Incorrect co-location for action condition when the active partner is on the non-extinguished side*. There was an interaction between the perspective and the side of the reported item, $\chi^2(1) = 23.39$, $p < .001$; the likelihood ratio of the model was, $\chi^2(0) = 0$, $p = 1$. There was better reporting of the non-extinguished than the extinguished item, and there were more reports of single items in the 1PP than in the 3PP.
4. *Incorrect co-location for action condition when the active partner is on the extinguished side.* There was a final model with a likelihood ratio of, $\chi2(0) = 0$, $p = 1$. There was a reliable interaction between the perspective and the side of the reported item, $\chi2(1) = 24.11$, $p < .001$. In this case the interaction arose because the difference between reporting the non-extinguished and extinguished stimuli was greater when the stimuli were seen in the third-person compared to the 1PP; there were relatively more reports of the extinguished (active) item in the 1PP compared to the 3PP.

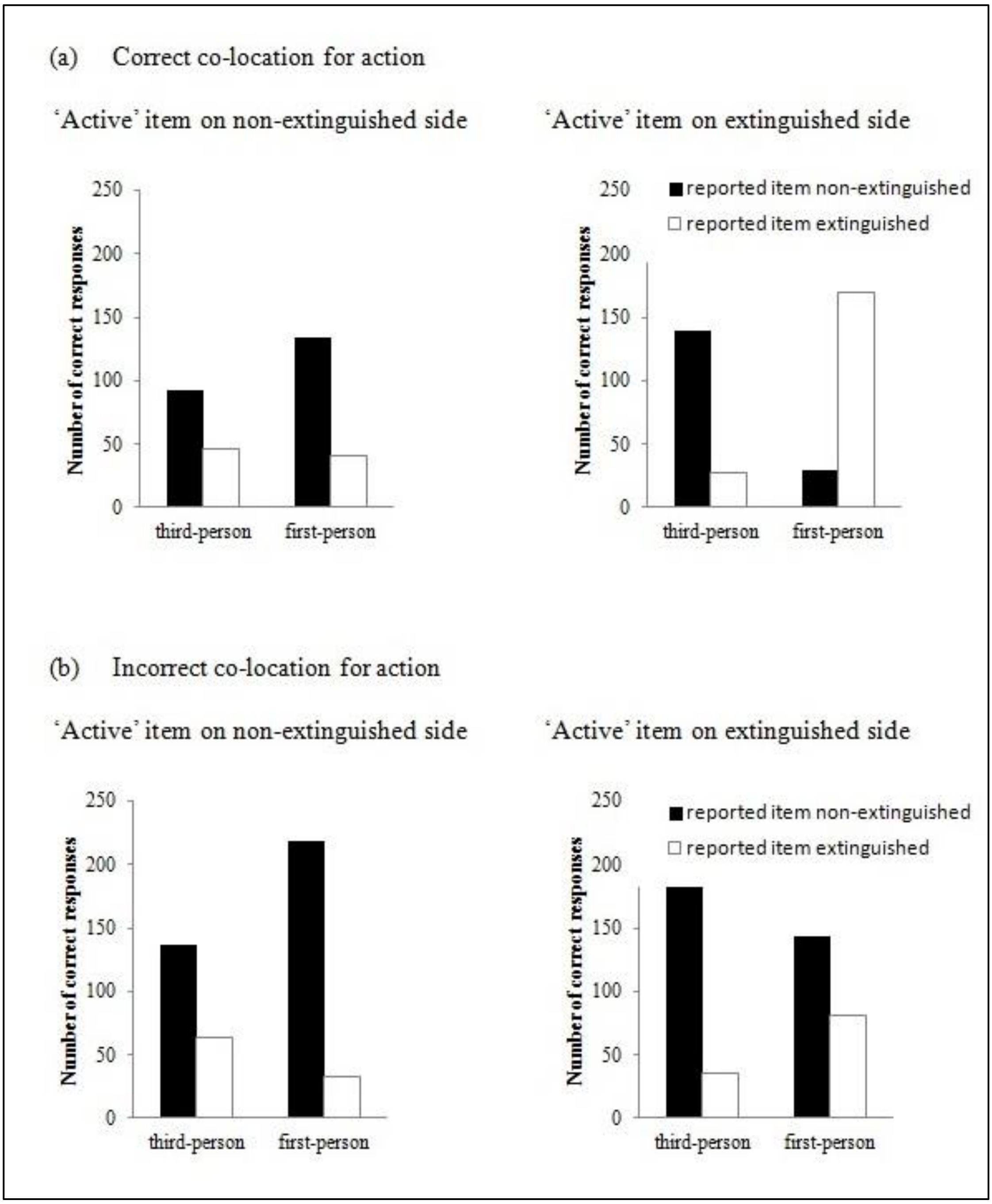
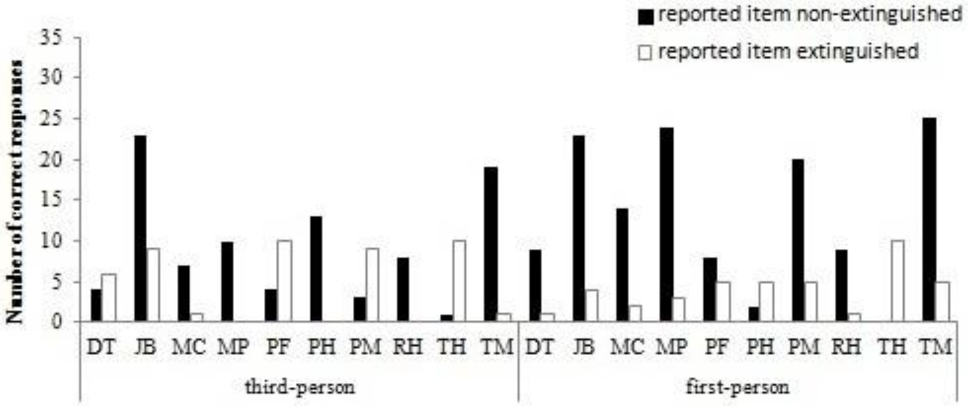


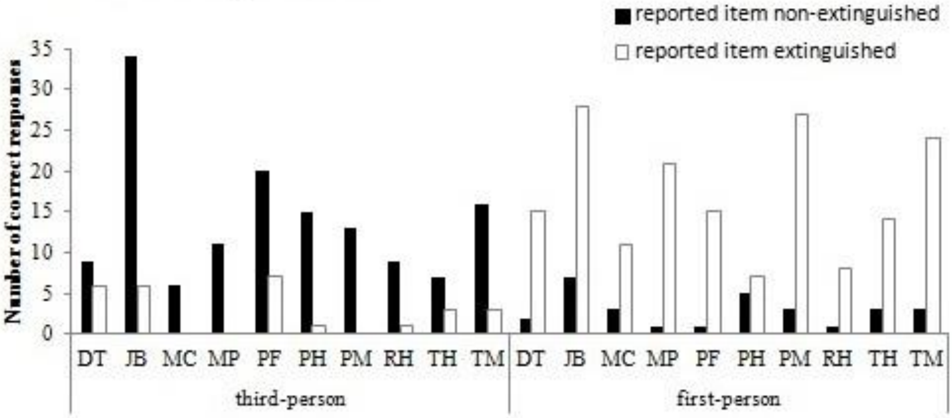
Figure 4.7. Number of correct responses for two-item trials when only one item of an object pair was reported (either on the non-extinguished or on the extinguished side) as a function of the position of the active partner of the pair (either on the non-extinguished or on the extinguished side) and whether the (a) objects were correctly or (b) incorrectly co-located for action.

(a) Correct co-location for action

'Active' item on non-extinguished side



'Active' item on extinguished side



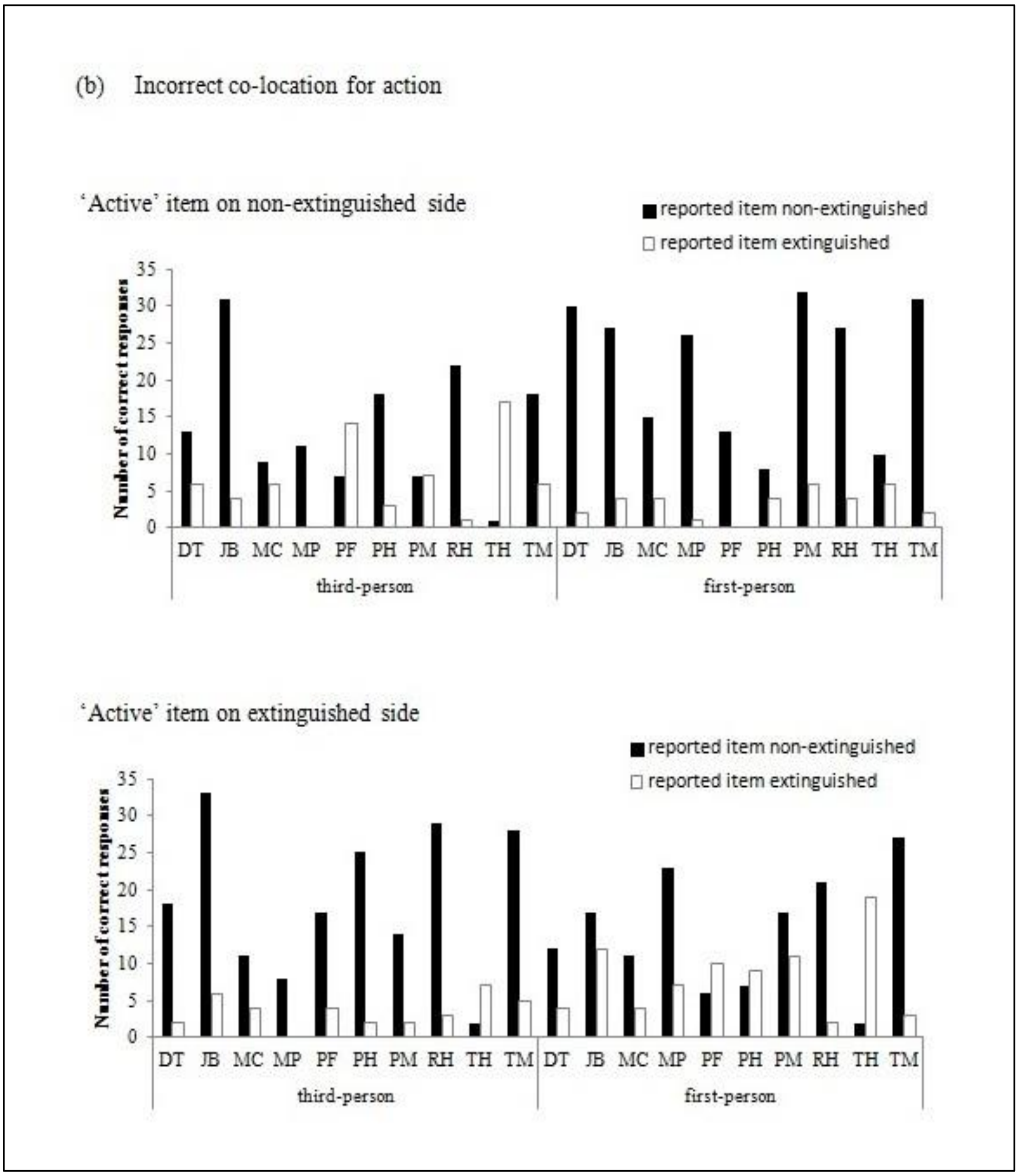


Figure 4.8. Individual performance when only one item of an object pair was correctly reported, for the correct (a) and incorrect (b) co-location for action conditions, as a function of whether the active item appeared on the non-extinguished or on the extinguished side.

4.5 Discussion

The present chapter extended the behavioural findings of Riddoch et al. (2003) and Humphreys et al. (2010a) who established that visual extinction is less severe when familiar objects were arranged in the correct co-locations for action relative to when they were incorrectly positioned for action. Here we investigated whether the effects of positioning objects for action extended to objects that were not typically used together.

The main results of this chapter can be summarised as follows: Firstly, patients were better at identifying two objects which were correctly positioned for action relative to those which were incorrectly positioned. This finding confirms that patients did benefit from the action relation between the objects and thus, recovered from extinction. Moreover, this replicates the basic finding by Riddoch et al. (2003) and confirms that the effects of action relation are found even with object pairs that are unfamiliar together (see also Riddoch et al., 2006, for prior patient data, and Roberts & Humphreys, 2011, for results from normal participants). The fact that unfamiliar pairs of objects reduced extinction suggests that the "potential for action" (visual affordance offered by the functional relationship) rather than learned knowledge about the object pair is important for the effect (Humphreys & Riddoch, 2007; Riddoch et al., 2006). This proposal is consistent with the affordance account provided by Gibson (1979) who claims that our perception is influenced by the visual affordances offered by the environment. In other words, there is a direct link between the perceptual properties of an object and the action that might be performed on it, regardless of the observer's intention to act. Secondly, the benefit for correctly positioned object pairs was apparent in both the 1PP and the 3PP, replicating the results by Humphreys et al. (2010a). However, in this case the recovery from extinction was greatest when the objects were depicted from a 3PP relative to a 1PP, irrespective of whether the objects were grasped by hands congruent or incongruent with those the patient would use to perform the action. This differs from the pattern found with familiar object pairs: For familiar pairs there was less extinction when objects appeared from a 1PP than a 3PP, and when the objects were grasped by hands congruent with those used by the patient (Humphreys et al., 2010a).

The 3PP advantage for pairs of unfamiliar objects is surprising as we might expect that our visual experience is greatest when objects are seen from a 1PP rather than from a 3PP (the biologically realistic posture of the stimuli here which corresponded well with the patient's 1PP). Both the familiarity of the view, and the matching of the participant's own action, would be expected to enhance the report. So why did patients perform better when objects appeared from a 3PP compared to a 1PP? The analysis of the error trials, where only one item of the object pair was reported, might help to explain this finding. One possibility is that the 1PP condition biased attention to the active object in the pair. When the active object fell on the non-extinguished side, this could increase the pathological bias to favour the non-extinguished side and could lead to delayed or no identification response to stimuli on the opposite side, resulting in extinction particularly when the objects were not related to action. Similarly if attention was cued to an active object on the extinguished side (as suggested by the error analysis with action related pairs; see below), then extinction could increase because the identification of the extinguished item takes significantly longer before attention can be switched towards the non-extinguished item. In addition, the report of the item on the non-extinguished side might suffer due to an overall pathological decrease in processing capacity (Robertson & Frasca, 1992).

These arguments about attention being cued to the active object fit with perhaps the most striking present results, those in the error analysis. When objects were (i) co-located for action, (ii) seen from a 1PP and (iii) the active object was on the extinguished side, there was better report of the extinguished than non-extinguished item – a reversal of the standard pattern of extinction. This noteworthy finding replicates the results by Riddoch et al. (2003). A similar but weaker pattern was observed when objects were not co-located for action. The advantage for reporting the active object is consistent with the suggestion by Handy et al. (Handy & Tipper, 2007; Handy et al., 2003) that tools bias spatial attention to their locations. This might be the case in the present study and in Riddoch et al.'s study (2003). When the objects were co-located for action, patients even reported more extinguished tools (the active partner) than non-extinguished objects (the passive partner) in error trials. This implies that action relations influence perception even when patients were not aware of the simultaneous stimulus presentation since, on these error trials, patients only reported the presence of one object.

The bias for reporting the tool is in general accord with the proposal that tools are a special category of object. Several studies have shown that the mere viewing of tools relative to other objects (animals, faces, houses, and shapes) automatically activates action representations associated with tool use or that are afforded by their visual properties such as orientation or graspability, even when no response is required (e.g., Gallivan, McLean, & Culham, 2011; Chouinard & Goodale, 2010; Vingerhoets et al., 2009; di Pellegrino et al., 2005; Phillips & Ward, 2002; Chao & Martin, 2000; Tucker & Ellis, 1998). This indicates that the visual properties of the tool are particularly effective in potentiating actions and, in turn, influencing visual selection (cf. Gibson, 1979).

The tendency for active objects being more reported fits also well with temporal order judgement studies. Participants were faster in detecting the active object when the objects were action-related compared to when they were not (Roberts & Humphreys, 2010b; see also Roberts & Humphreys, 2011a). This temporal order bias would follow from attention being drawn to the active object in action-related pairs. That the present result arose primarily only for correctly co-located object pairings, and only when objects were seen from a 1PP, is also important. It suggests that the combination of co-locating objects for action and viewpoint is what is critical for the attentional bias to emerge. The attention system responds to encountering an action unit based on objects co-located for the participant's own action.

On top of these effects of relatedness and perspective, there was an effect of object-hand congruence. Surprisingly, the effects of action relation were stronger for some patients when the objects were incongruently aligned with the patient's handedness. This result goes against the motor-based affordance account of performance (Humphreys et al., 2010b). According to this account, report should be better when objects are held in a manner congruent rather than incongruent with the patient's habitual action. It may be, however, that object-hand congruence biased the patient's attention to the matching (usually right) side, and this disrupted report – at least when the objects did not form a sufficiently familiar pair to counter-act such a bias. Whereas any effects of hand congruence here were weak, Humphreys et al. (2010a) reported strong effects with familiar object pairs. Such a contrast suggests that motor-based affordance responses are more likely with familiar objects, while visual familiarity with the participant's own reference frame may operate for unfamiliar as well as familiar objects positioned for action.

4.6 Conclusion

The results of the present chapter indicate that unfamiliar action relations between objects ameliorate visual extinction. With unfamiliar object pairs, the effects of perspective and object-hand congruence are less pronounced (or even opposite to) the effects found with familiar objects, suggesting that affordances (indexed by the perspective and object-hand congruence effects) are stronger with familiar objects. In addition, with object pairs positioned for action and seen from a 1PP, attention was biased to the active member of the pair (the tool), even if it fell on the extinguished side. The results indicate that the effects of action relations on attention may reflect several factors, determined by the familiarity of the object pairs, the viewpoint and whether objects are co-located for action.

CHAPTER 5: EFFECTS OF BROKEN AFFORDANCE ON VISUAL EXTINCTION[1]

5.1 Abstract

Previous studies (including Chapter 4) have shown that visual extinction can be reduced if two objects are positioned to afford an action. In this chapter it was tested if this affordance effect was disrupted by "breaking" the affordance, i.e., if one of the objects actively used in the action had a broken handle. We tested eight patients with right hemisphere lesions and left-sided extinction. Patients viewed object pairs that were or were not commonly used together and that were positioned for left- or right-hand actions. In the unrelated pair conditions, either two tools or two objects were presented. In line with previous research (e.g., Riddoch et al., 2006), extinction was reduced when action-related object pairs and when unrelated tool pairs were presented compared to unrelated object pairs. There was no significant difference in recovery rate between action-related (object-tool) and unrelated tool pairs. In addition, performance with action-related objects decreased when the tool appeared on the ipsilesional side compared to when it was on the contralesional side, but only when the tool handle was intact. There were minimal effects of breaking the handle of an object rather than a tool, and there was no effect of breaking the handle on either tools or objects on single item trials. The data suggest that breaking the handle of a tool lessens the degree to which it captures attention, with this attentional capture being strongest when the tool appears on the ipsilesional side. The capture of attention by the ipsilesional item then reduces the chance of

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[1] Chapter 5 is an adapted version of Wulff, M., & Humphreys, G. W. (2015). Effects of broken affordance on visual extinction. *Front Hum. Neurosci., 9,* 515. doi:10.3389/fnhum.2015.00515.

detecting the contralesional stimulus. This attentional capture effect is mediated by the affordance to the intact tool.

5.2 Introduction

Previous studies have shown that the perceptual properties of single objects afford certain actions, and this in turn influences visual attention and perception. This affordance effect (Gibson, 1979) reflects the action possibilities offered by the environment to the observer, depending upon the observer's current goal and his/her action capabilities. For example, a cup will strongly afford a drinking action when we are thirsty and are able to grasp it, but not if we just have quenched our thirst and the cup is positioned inappropriately for the action (e.g., Humphreys & Riddoch, 2001). Such affordances are determined by the perceptual properties of the object such as the size and orientation of the cup. Thus for a right-handed person a cup is more likely to afford an action when its handle is oriented to the right than when it is oriented to the left, even though the object can be recognised equally efficiently in the different orientations (Riddoch, Edwards, Humphreys, West, & Heafield, 1998).

The affordance effect is of particular relevance for patients showing visual extinction, a neuropsychological disorder commonly observed following damage to the right posterior parietal cortex (Chechlacz et al., 2014; Karnath et al., 2003). Extinction patients are able to detect a single contralesional stimulus presented in isolation but frequently fail to detect a contralesional stimulus when an ipsilesional stimulus appears simultaneously. Several behavioural studies have demonstrated that extinction can be modulated by grouping on the basis of Gestalt principles such as similarity and collinearity (e.g., Gilchrist et al., 1996). There are also higher-order influences on extinction which act even in the absence of Gestalt grouping factors. For example, extinction can be reduced when patients view pictures displaying objects oriented for left-hand or right-hand actions. Di Pellegrino et al. (2005) first showed that the orientation of an object handle influenced stimulus detection, with less extinction when the contralesional object afforded a left-hand rather than a right-hand grasp. Di Pellegrino et al. (2005) suggested that affording an action to the left reduced extinction.

Apparently similar affordance effects on extinction can be observed with pairs of objects. Riddoch et al. (2003) presented pictures of objects either positioned to interact with each other or not. There was less extinction when objects appeared in the correct co-locations for action (a fork and knife facing each other) relative to when the same objects were positioned incorrectly for action (a knife facing away from a fork). Riddoch et al. (2003) concluded that interacting objects offer an affordance which groups the objects for attentional selection, enabling the constituent stimuli to be selected as a single unit. As a result, the perceptual report of both stimuli is improved and extinction is less severe. Several studies have reported similar results with healthy participants, with performance improving when objects are action-related compared to when they are unrelated (Borghi et al., 2012; McNair & Harris, 2012; Roberts & Humphreys, 2011a; Roberts & Humphreys, 2011b; Adamo & Ferber, 2009; Green & Hummel, 2006). For example, Roberts and Humphreys (2011a) showed healthy participants briefly presented objects and found improved identification performance when objects were in correct relative to incorrect co-locations for action.

Several behavioural studies have demonstrated that affordance effects for single (graspable) objects can be manipulated by factors such as object size (e.g., Tucker & Ellis, 2001), object location in space (e.g., Costantini et al., 2010), object orientation (e.g., Goslin et al., 2012; Tucker & Ellis, 1998), and hand-object congruence (e.g., Girardi, Lindemann, & Bekkering, 2010). However, it seems that the position and graspability of the object handle is particularly important for affordance effects (cf. Matheson et al., 2014; Symes et al., 2007). Notably, the spatial location of the handle influences stimulus identification as demonstrated in neglect patients (Humphreys & Riddoch, 2001), extinction patients (di Pellegrino et al., 2005), and healthy participants (e.g., Tucker & Ellis, 1998). In addition, performance can also be affected by disrupting graspability by breaking the handle of an object. Buccino et al. (2009) applied TMS over the left motor area in healthy participants. Participants viewed pictures of objects with an intact and a broken handle oriented to the right and the left side. Objects with an intact right oriented handle evoked a larger motor response compared to objects with a broken right oriented handle. The decrease in the motor response with broken handles relative to intact handles suggests that not only the handle orientation but also whether it is intact or not is crucial for the perception of affordance. Buccino et al. (2009) proposed that the graspability of an object may be processed in the motor cortex. Objects with an intact handle will be processed as being graspable and the corresponding motor representations will be automatically activated, whereas objects with a broken handle will be coded as less graspable and thus there will be reduced activation of the motor cortex. Graspability also influenced responses in a probe detection task (Garrido-Vasquez & Schuboe, 2014), with faster probe detection times when the cued object was graspable (cup) compared to when the cued object was non-graspable (cactus). Whether such effects also occur in extinction patients has not been examined, nor is it clear whether effects of breaking a handle modulate how we attend to objects. It is possible that the coding of action-related pairs of objects operates using relatively coarsely coded visual representations, where the graspability of individual objects (and the presence of a broken handle) is less critical. Here we might expect a broken handle to reduce attentional responses to paired, action-related objects.

There are also data indicating that attention can be biased within pairs of action-related objects. Notably, when only one member of an object pair is reported by patients showing extinction, this tends to be the object that was active in an action (typically the tool that was used to act on the other object; Wulff & Humphreys, 2013; Riddoch et al., 2003). This bias can occur even when the active object falls in the contralesional field. In addition, normal participants tend to judge that the active member of an action-related pair appears first, when asked to make temporal order judgements (Roberts & Humphreys, 2010b). Both findings are consistent with attention being attracted to the active tool, within an action-related pair. The preferential report for tools has subsequently been replicated with healthy participants using various experimental paradigms (Wulff et al., 2015; Laverick et al., 2015; Xu et al., 2015; McNair & Harris, 2014; Roberts & Humphreys, 2011a; Roberts & Humphreys, 2010b). Thus, breaking the handle of the tool may have a greater effect on report than breaking the handle of the passive, action recipient. For example, the attentional bias to the active tool may be reduced.

In the present chapter, we assessed the impact of a broken handle on the effects of affordance on extinction. To do this, we evaluated whether the effect of action relations on visual extinction holds when object pairs appear and one of the stimuli has a broken handle. In contrast to other studies (e.g., Humphreys et al., 2010a), we only presented pairs of objects in correct co-locations for action. We predicted that the affordance effect is stronger for familiar (action-related) rather than for unfamiliar (unrelated) pairs of objects (cf. Riddoch et al., 2006). Also, if the graspability of individual objects is important, we expected that the affordance effect would be reduced with broken object pairs compared to intact object pairs as previous studies have shown that viewing non-graspable (broken-handled) objects can eliminate motor-based affordance effects (Buccino et al., 2009). We further predicted differences according to whether a tool or an acted-upon object had a broken handle (cf. Wulff & Humphreys, 2013; Riddoch et al., 2003). Breaking the handle of a tool should be more disruptive to performance than breaking the handle of a passive object, in an action-related pair.

5.3 Methods

5.3.1 Patients

Eight patients with visual extinction from 55 to 78 years of age (2 females, M = 66.88; SD = 8.15) were recruited from the volunteer panel at the University of Birmingham. Six patients had right unilateral lesions and two had bilateral lesions (clinical details are given in Table 5.1). All the patients showed left visual extinction on the BCoS Cognitive Screen (Humphreys et al., 2012)[i]. The patients did not have visual field defects on visual confrontation testing or suffered from optic ataxia. Three patients (P1, P3, and P6) showed mild apraxia on the BCoS (see Table 5.1). However, the extinction data for these patients were not clearly different from the results of the other patients; similarly there were no differences between the extinction results for the unilateral and bilateral cases. All reported normal or corrected-to-normal vision. Informed consent was obtained from all patients and the study was approved by a national NHS research ethics committee.

Table 5.1 Demographic and clinical data of the patients

Patient	Sex / age / handedness	Main lesion site	Major clinical symptoms	Time since lesion (years)
P1	F / 76 / L	Right parieto-temporo-frontal cortex; left occipital cortex	Left extinction; neglect in reading and writing; problems with gesture recognition, gesture production and gesture imitation	13
P2	M / 78 / R	Right occipito-parieto-temporal cortex extending to the inferior frontal gyrus	Left neglect; left extinction	5
P3	F / 63 / R	Bilateral lesions to the posterior parietal cortices extending more inferiorly in the left hemisphere	Left extinction; dysgraphia; problems with gesture imitation	> 10
P4	M / 70 / R	Bilateral parietal cortices and right superior temporal gyrus	Left extinction	> 4
P5	M / 58 / R	Right fronto-parieto-temporal cortex (middle frontal gyrus, angular gyrus, supramarginal gyrus, middle and superior temporal gyrus)	Left extinction	4
P6	M / 70 / R	Right fronto-temporal cortex extending to the parietal cortex (inferior parietal gyrus, angular gyrus, supramarginal gyrus)	Left extinction; problems with gesture imitation	5
P7	M / 55 / R	Right parieto-temporo-frontal cortex	Left extinction	1
P8	M / 65 / L	Right parietal cortex and bilateral subcortical regions (putamen, pallidum)	Left extinction	3

Note. M = male; F = female; R = right; L = left.

5.3.2 Apparatus and stimuli

Four coloured photographs of common drinking containers were used (flask, teapot, cup, and beaker). Each item was photographed on a table with the handle orienting to the right, and then flipped within the horizontal plane in Microsoft Office Picture Manager (Version 12) to create a mirror image of each item. Thus, an item with a right-oriented handle was turned into an item with a left-oriented handle. A second set of images in which each item had a broken handle was created using Paint.NET (Version 3.5.10). This resulted in 2 (handle: intact, broken) x 2 (handle orientation: right, left) x 2 (stimulus type: object, tool) images. The tools and non-tool objects were not matched for size as this manipulation might have disrupted the effect of action relation (cf. Riddoch et al., 2011). However, variations across the individual stimuli should not have been critical as items were counter-balanced across conditions.

The individual items were organised into pairs with the items positioned to interact with each other with their handles facing outwards. There were three object pair conditions with each object pair either familiar or unfamiliar to the patient (see Figure 5.1). The objects were: (i) action-related: a tool and an object that were commonly used together (teapot and cup; beaker and flask); (ii) an unrelated pair in which two tools were presented (teapot and flask) and (iii) an unrelated pair in which two objects were presented (beaker and cup). Note that in this study action relation relates to the familiarity with the object pair rather than to the co-location for action. For the action-related pair, each object within the pair was classified as being either the active or the passive member of the pair (cf. Riddoch et al., 2003). In the "intact handle condition", all the objects had an intact handle, while in the "broken handle condition" one item within the pair had a broken handle. This was the active tool for half of the stimuli, and the passive object for the other half. The items were arranged either with (i) the tool on the right side and the object on the left side or with (ii) the tool on the left side and the object on the right side. Note that the side of extinction could correspond to the side of the tool or not. Each item pair was presented simultaneously, one item to the right and the other item to the left side of fixation. The stimuli appeared on a black background.

One-item trials were randomly intermingled with the two-item trials. Here, an item (either with an intact or a broken handle) was paired with a blank table on the other side of fixation (to maintain approximate levels of visual stimulation), and it was presented at the same location and for the same duration as it appeared on two-item trials.

Items were displayed on a 19-inch monitor at a viewing distance of approximately 50 cm. The monitor provided a frame refresh rate of 60 Hz with a spatial resolution of 1024 x 768 pixels. The stimuli subtended 10.29° x 8.56° of visual angle and were located 0.86° either to the left or right side of central fixation. We positioned the items very centrally to imply a joint action between the two objects in the action-related condition. The average distance between the centre of both items was 12 cm (see also Ptak, Valenza, & Schnider, 2002; di Pellegrino & De Renzi, 1995).

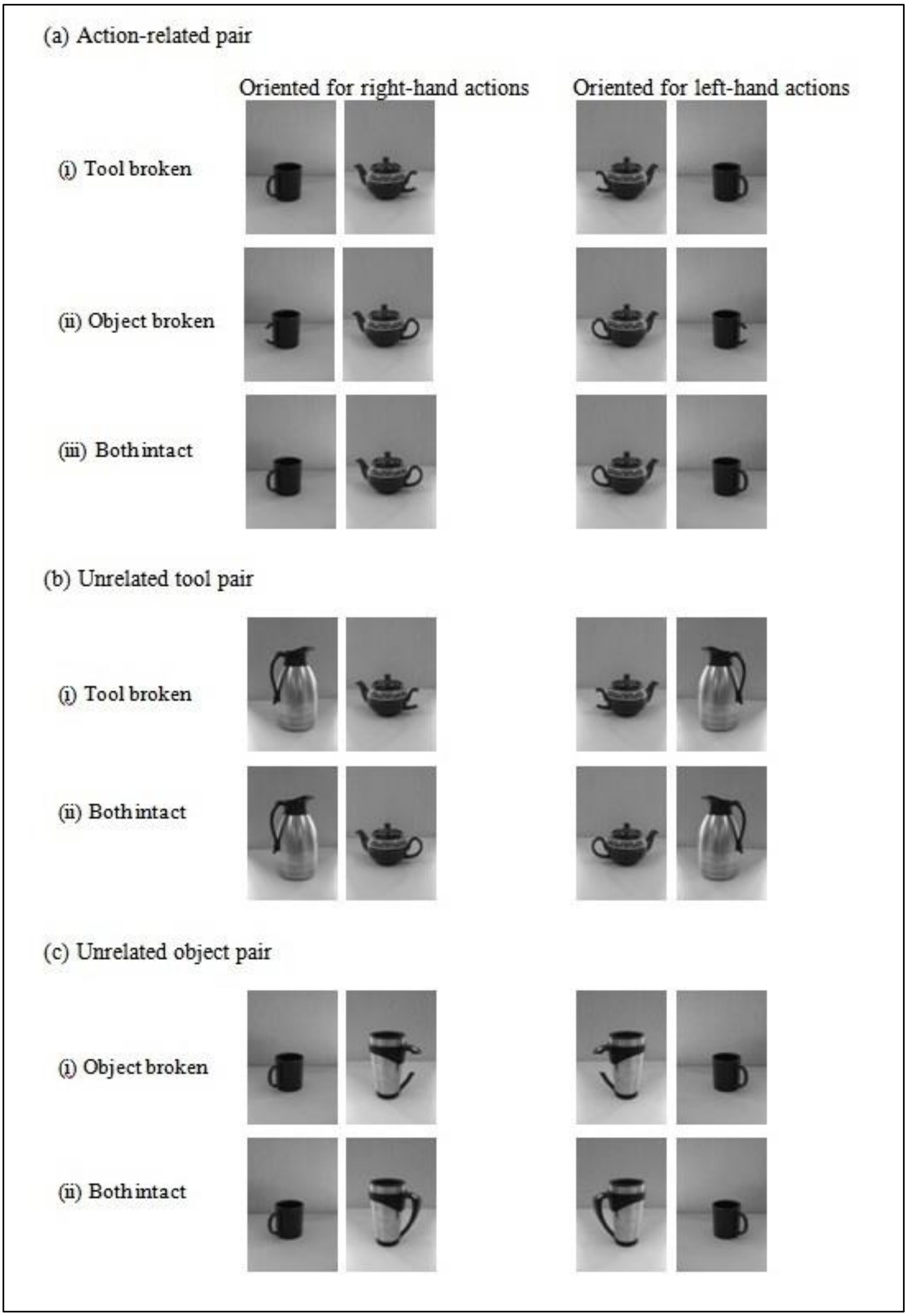

Figure 5.1. Examples of two-item stimuli presented either as action-related pairs (object-tool pair) (a), unrelated tool-tool pairs (b) or as unrelated object-object pairs (c). The stimuli are shown with a broken handle on the contralesional side (left panels) or with a broken handle on the ipsilesional side (right panels).

5.3.3 Design and procedure

A similar design to Humphreys et al. (2010a) and Wulff and Humphreys (2013) was used. The experiment consisted of two conditions (Intact objects and Broken objects), which were administered to each patient in an ABAB order across three sessions, with at least one week apart. The order of the conditions was counterbalanced across patients.

The two conditions were identical with the exception that in the Broken handle condition, one member of the pair had a broken handle, whereas in the Intact handle condition the handles of both stimuli were intact. The Broken handle condition consisted of eight bilateral conditions [condition (action-related, unrelated tool, unrelated object) x handle (tool broken, object broken) x side of tool (contralesional, ipsilesional)] and eight unilateral conditions [stimulus type (object, tool) x handle (tool broken, object broken) x side (ipsilesional, contralesional)]. There were 768 trials which were presented in 12 blocks of 64 trials; 48 trials for each condition. The Intact condition consisted of six bilateral conditions [condition (action-related, unrelated tool, unrelated object) x side of tool (contralesional, ipsilesional)] and four unilateral conditions [stimulus type (object, tool) x side (ipsilesional, contralesional)]. There were 384 trials which were presented in six blocks of 64 trials; 48 trials for each condition. Each stimulus was repeated eight times within one block. In prior studies of the effects of affordance on extinction only a small number of items have been used (e.g., di Pellegrino et al., 2005) in order to allow a clear and controlled manipulation of the main factors of interest. In both the Intact and the Broken handle conditions one-item and two-item trials were fully randomised.

Patients had to identify and name the item(s) on each trial by verbal report. Patients were tested individually in a quiet room. Responses were recorded as correct if either the single item was correctly named, or if both items were correctly named on bilateral trials. It was also noted whether one item on two-item trials was correctly reported, while we did not separately record (i) whether patients reported the presence of a second item which they could not name or (ii) named the second item incorrectly, or (iii) whether they thought only one item was present. However, we also recorded whether any item on two-item trials was reported. Before each session, pictures of the stimuli were presented individually on a monitor to each patient to ensure that the patients could recognise and correctly identify the items. Additionally, patients were given at least 14 practice trials to ensure adequate performance in the task and the stimuli on these practice trials were different from those employed in the experimental trials to avoid carry-over effects. During these practice trials, stimulus exposure time was adjusted to ensure that each patient achieved a performance level of roughly 70-90% correct for single items in the contralesional hemifield (Table 5.2) before the experimental trials began. The practice trials were repeated until this level was achieved across a block of 14 trials; the exposure duration was then fixed for a patient for each session.

Each trial began with a white central fixation cross presented on a black background for 2000 ms, which was replaced by a red fixation cross for 500 ms to inform patients that the stimulus was about to appear. Next a single object or an object pair was presented. For all patients (except P1, P6, and P7) a 100 ms mask followed the object(s) to maintain the same level of task difficulty across patients. Responses were manually recorded by the experimenter, and after that the next trial was initiated.

Table 5.2 Stimulus exposure times for the Intact (unbroken handles) and the Broken handle condition

Patient	Intact (unbroken handles) condition (ms)	Broken handle condition (ms)
P1	M = 267 (Session 1: 300, Session 2: 200, Session 3: 300)	M = 267 (Session 1: 300, Session 2: 200, Session 3: 300)
P2	100 + 100 Mask	M = 167 + 100 Mask (Session 1: 150 + 100 Mask, Session 2: 100 + 100 Mask, Session 3: 100 + 100 Mask)
P3	M = 133 + 100 Mask (Session 1: 100 + 100 Mask, Session 2: 150 + 100 Mask, Session 3: 100 + 100 Mask)	M = 133 + 100 Mask (Session 1: 150 + 100 Mask, Session 2: 100 + 100 Mask, Session 3: 150 + 100 Mask)
P4	200 + 100 Mask	200 + 100 Mask
P5	M = 92 + 100 Mask (Session 1: 100 + 100 Mask, Session 2: 75 + 100 Mask, Session 3: 100 + 100 Mask)	M = 83 + 100 Mask (Session 1: 100 + 100 Mask, Session 2: 75 + 100 Mask, Session 3: 75 + 100 Mask)
P6	150	M = 167 (Session 1: 200, Session 2: 150, Session 3: 150)
P7	M = 767 (Session 1: 1400, Session 2: 500, Session 3: 400)	M = 583 (Session 1: 1100, Session 2: 250, Session 3: 400)
P8	M = 167 + 100 Mask (Session 1: 150 + 100 Mask, Session 2: 150 + 100 Mask, Session 3: 200 + 100 Mask)	M = 233 + 100 Mask (Session 1: 200 + 100 Mask, Session 2: 200 + 100 Mask, Session 3: 300 + 100 Mask)

Note. M = Mean.

5.4 Results

We analysed accuracy data as well as error data. Accuracy data reflect correct naming of a single item in unilateral and of two items in bilateral trials. These data were used to contrast report on one- and two-item trials, and thus to assess whether extinction occurred. For two-item trials, error data were then computed by counting how many times only one of two items was correctly named (either on the left or right visual field), or no item was reported and whether the reported item fell on the ipsi- or contralesional side[1]. This was done to examine whether there was a preferential report of the tool. Note that errors when only one item was reported included three different response types: identification of one item and not reporting the second, identification of one item and reporting the presence of the second item which could not be named, and incorrect identification of the second item; cf. method section[2]. On average, patients made errors on 40% of the two-item trials, of which 38% were errors when patients only named one item correctly, while on just 2% of the trials patients failed to report any item. The former error type was used for all subsequent analyses. We report the results in several sections.

1. We assessed whether there was a spatial extinction effect by testing performance overall on two-item vs. one-item trials, separately for the intact and the broken handle conditions.
2. We investigated the effects of action relation on two-item report, comparing action-related (familiar) and unrelated (unfamiliar) object pairs when the handles were intact. This attempts to replicate prior work (cf. Riddoch et al., 2003). We also explored whether there are differences between the three types of object pairs in their error pattern, i.e., when only one item was correctly reported.
3. We examined the role of broken handles on two-item trial performance. This was done in three stages: (i) We evaluated the effects of having a broken handle on performance only with action-related objects: first when the tool handle was broken and then when

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[1] Note that the accuracy data could not be used since these data failed to distinguish which item was reported on an error trial.

[2] Unfortunately we failed to record the type of error when only a single item was reported. However it should be noted that by far the majority of such errors involved patients reporting one item and making no response to the other.

the object handle was broken. (ii) We assessed the contrast between action-related objects and unrelated tools when the tool handle was broken. (iii) We examined the contrast between action-related objects and unrelated objects when the object handle was broken. These latter two contrasts are the same as comparison (2) above, except that one of the stimuli had a broken handle here, whereas the handles were intact in comparison (2). (iv) We also explored whether patients tended to report more tools or objects on error trials when only one item was correctly named, in the action-related condition (when tools and objects were paired together).

4. Finally, we assessed whether there were differences in reporting unilateral tools vs. unilateral objects.

In all analyses, we included patient as a between-subject factor (with sessions as subjects) to test whether there are variations in the size of the effects across patients. Greenhouse-Geisser correction for degrees of freedom was used when the assumption of sphericity was not met. Significant differences between conditions were further assessed with paired *t*-tests ($p < .05$).

5.4.1 The presence of extinction

We compared performance on one-item trials with performance on two-item trials to confirm that patients suffered from extinction, with extinction being present when patients' identification performance was significantly better on one-item than on two-item trials. The accuracy data from one-item trials and from the different two-item conditions (pooled across conditions), based on the number of items correctly reported on the ipsilesional or contralesional side, were entered into an ANOVA with the within-subject factors being number of objects (one-item, two-items) and side of item being reported (ipsilesional, contralesional); patient was treated as a between-subject factor.

Intact condition. Performance on one-item trials was significantly better than performance on two-item trials, confirming that visual extinction was present, F(1,16) = 674.86, $p < .001$, $\eta_p^2 = .977$. The main effects of side, F(1,16) = 55.10, $p < .001$, $\eta_p^2 = .775$ (ipsilesional > contralesional stimuli) and patient, F(7,16) = 9.33, $p < .001$, $\eta_p^2 = .803$, were significant. The number of objects by side interaction, F(1,16) = 6.64, $p = .020$, $\eta_p^2 = .293$, reached significance. The side effect was slightly larger in the two-item trial conditions compared to the one-item trial conditions, though it was reliable for both, $t(23) = 4.96$, $t(23) = 4.63$, both $p < .001$, respectively (see Figure 5.2a). There were also significant interactions between the number of objects and patient, F(7,16) = 3.70, $p = .014$, $\eta_p^2 = .618$, between side and patient, F(7,16) = 3.44, $p = .019$, $\eta_p^2 = .601$, and between number of objects, side and patient, F(7,16) = 14.87, $p < .001$, $\eta_p^2 = .867$ (Figure 5.2b). These interactions indicate that the extinction effect was larger for some patients than for others, though all patients showed extinction and patients' performance varied as a function of the side of stimulus.

Broken handle condition. The same ANOVA was conducted with broken object pairs. As with intact object pairs, identification performance was significantly better on one-item than on two-item trials, F(1,16) = 1395.25, $p < .001$, $\eta_p^2 = .989$ (Figure 5.2c). There were significant main effects of side, F(1,16) = 75.21, $p < .001$, $\eta_p^2 = .825$ (ipsilesional > contralesional stimuli) and patient, F(7,16) = 8.34, $p < .001$, $\eta_p^2 = .785$. The number of objects by side interaction, F(1,16) = 4.81, $p = .043$, $\eta_p^2 = .231$, was also significant. As before, the side effect was slightly larger in the two-item trial conditions compared to the one-item conditions, $t(23) = 4.74$, $t(23) = 4.17$, both $p < .001$, respectively. There were also significant interactions between the number of objects and patient, F(7,16) = 3.55, p = .017, $\eta_p^2 = .608$, between side and patient, F(7,16) = 6.55, p = .001, $\eta_p^2 = .741$, and between number of objects, side and patient, F(7,16) = 11.50, $p < .001$, $\eta_p^2 = .834$. The variations across patients are shown in Figure 5.2d; however the one item advantage was present for all patients.

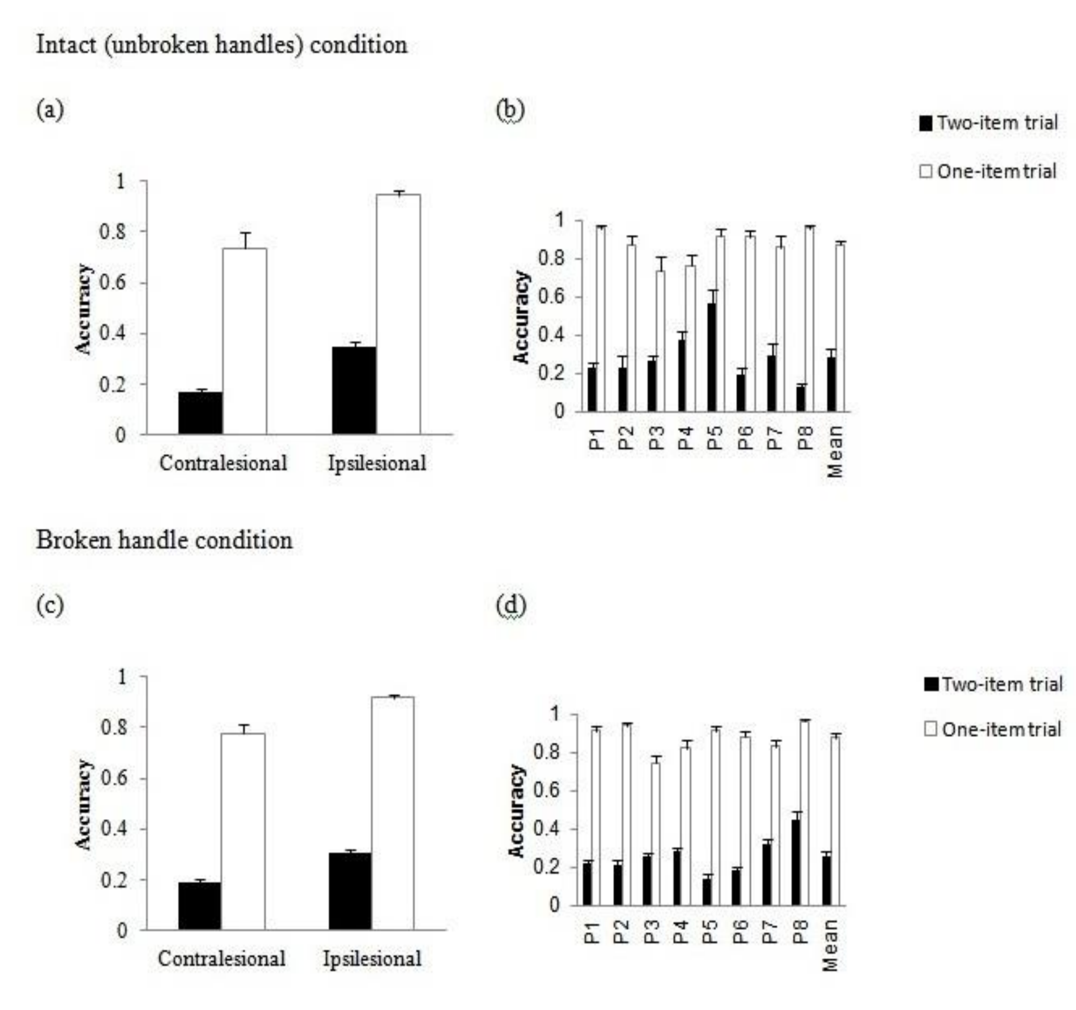

Figure 5.2. Data for one-item and two-item trials in the Intact (unbroken handles) condition and in the Broken handle condition as a function of side of stimulus. Mean accuracy of performance (a, c) and mean patient accuracies (b, d) with error bars indicating standard error (SE).

5.4.2 Effects of object pair type on two-item report (intact handles)

Accuracy data. To investigate whether the type of object pair affected identification performance when both handles were intact, the data from action-related (object-tool) pairs were compared with unrelated tool-tool and with unrelated object-object pairs. Figure 5.3a shows the mean performance for each object pair condition. The main effect of condition, $F(1.9,30.3) = 65.64$, $p < .001$, $\eta_p^2 = .804$, reached significance. Bonferroni corrected multiple comparisons showed that accuracy was significantly higher for action-related objects and for unrelated tools than for unrelated object pairs (both $p < .001$), whereas there was no difference between the report of action-related objects and unrelated tool pairs. The benefit for the related (object-tool) pair condition over the unrelated object-object pair condition indicates that the presence of the tool (in the action-related object-tool condition) benefitted report of the other (non-tool) object, and that action relatedness can benefit report (cf. Riddoch et al., 2003). There was also a benefit for two tools compared with two objects, indicating a general advantage for reporting tools. There was a significant main effect of patient, $F(7,16) = 5.19$, $p = .003$, $\eta_p^2 = .694$. The interaction between condition and patient, $F(13.3,30.3) = 9.00$, $p < .001$, $\eta_p^2 = .797$ (see Figure 5.3a), was reliable. This indicates that the magnitude of the effect of condition varied across individuals, but all patients showed the effect.

Error data. We compared the error data from these two-item trials when only one item of an object pair was correctly reported based on the side of the reported item (either on the ipsilesional or the contralesional side). A chi-square test indicated that the type of the object pair modulated the side of the reported item, $\chi^2(2) = 7.203$, $p = .027$, Cramer's $V = .127$. As can be seen in Figure 5.3b, the number of reported items on the ipsilesional relative to the contralesional side was higher for unrelated objects compared to action-related pairs and unrelated tools. This suggests that there is more “weight” placed during selection on the spatial position of the target when two objects are present relative to when one of the stimuli is a tool.

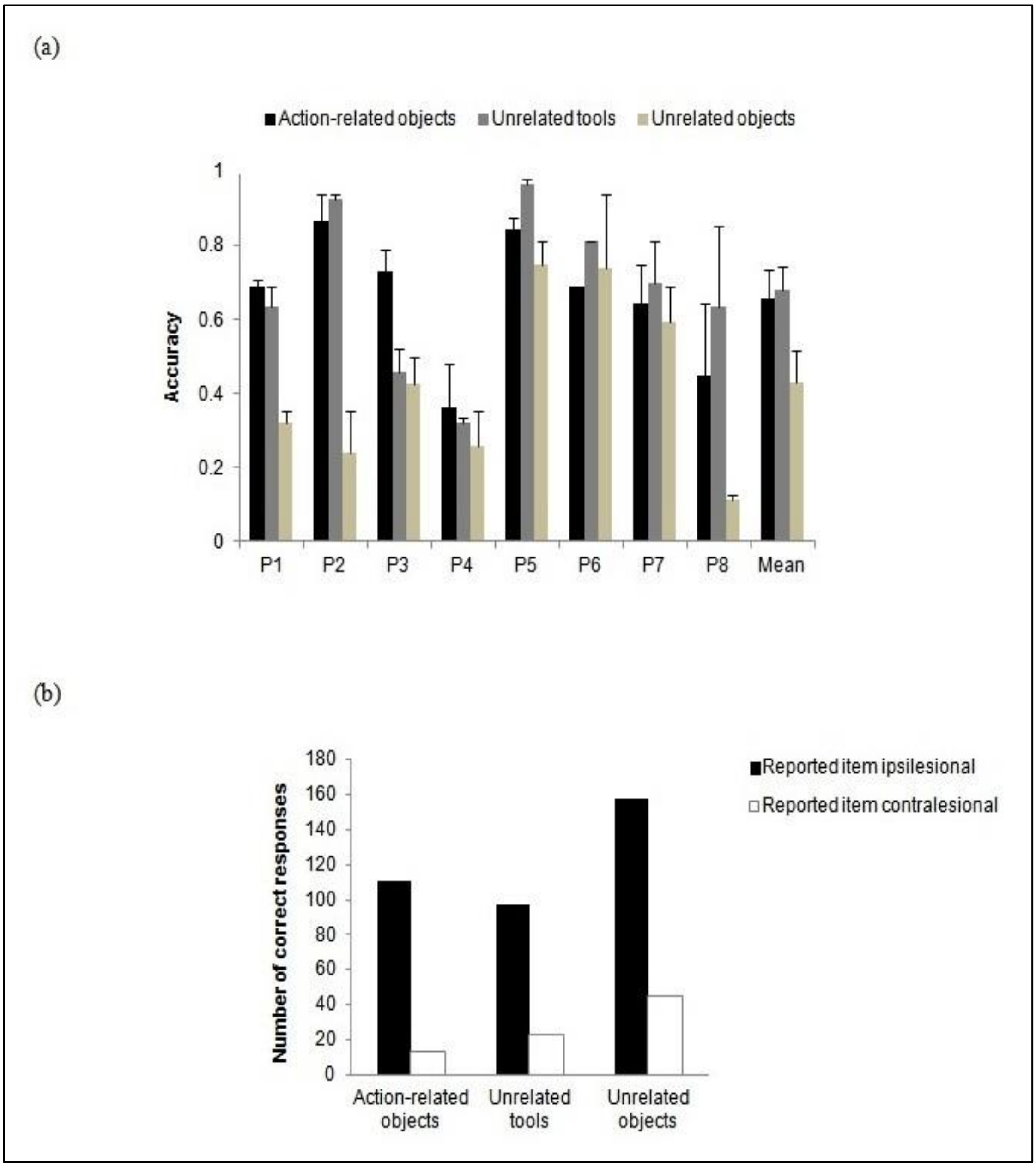

Figure 5.3. Intact handles only. (a) Mean patient accuracies and (b) number of correct responses for two-item trials when only one item of an object pair was reported (either on the ipsilesional or on the contralesional side) as function of object pair condition when both handles were intact. Error bars denote SE.

5.4.3 Role of broken handles on two-item trial performance

To assess whether a broken handle affected two-item trial performance, several separate ANOVAs were conducted with the factors being handle (both handles intact/one handle broken) and side of broken handle (contra- vs. ipsilesional); patient was treated as between-subject factor. Separate ANOVAs were conducted because the make-up of the conditions (e.g., two objects, two tools, object-tool – each sometimes having a broken handle) meant that the factors could not be nested in a single ANOVA.

(i) Effects with action-related objects only

First we assessed effects of having a broken tool handle; then we assessed effects of having a broken object handle. Finally, we analysed error trials to examine whether tools or objects are reported more often in error trials when only one item was correctly reported.

Tool handle broken (Figure 5.1a (i) vs. Figure 5.1a (iii)). There were reliable main effects of side of tool, F(1,16) = 9.33 , p = .008, $\eta_p^2 = .368$ (ipsilesional > contralesional) and patient, F(7,16) = 6.08 , p = .001, $\eta_p^2 = .727$. The interaction between intact/broken handle and side of tool was reliable, F(1,16) = 12.90, p = .002, $\eta_p^2 = .446$. When both handles were intact, there was better performance when the tool was presented on the contralesional side relative to when it was presented on the ipsilesional side, *t*(23) = 3.84, p = .001 (Figure 5.4a), while there was no reliable effect of the positioning of the tool when the tool handle was broken. The side of tool by patient interaction, F(7,16) = 2.84, p = .040, $\eta_p^2 = .554$, was also significant (Figure 5.4b). Patients differed in the degree to which they reported more stimuli when the tool was on the ipsilesional compared to when the tool was on the contralesional side; these effects were present for all but one patient (P1).

Object handle broken (Figure 5.1a (ii) vs. Figure 5.1a (iii)). There were significant main effects of intact/broken handle, F(1,16) = 4.90, p = .042, η_p^2 = .234 (broke > intact), side of broken handle, F(1,16) = 38.72, p < .001, η_p^2 = .708 (ipsilesional > contralesional) and patient, F(7,16) = 5.36 , p = .003, η_p^2 = .701. The effects of having a broken object handle and the side of the broken object handle were additive, F(1,16) = .634 , p = .438, η_p^2 = .038 (see Figure 5.4c). Note that the effect of the side of the broken object handle here fits with the effect of the tool position (above). Performance was better when the broken object handle was on the ipsilesional side (and the tool was on the contralesional side in the action-related pair) than when the broken object was on the contralesional side (and the tool was on the ipsilesional side). The interaction between the side of the broken object and patient was also reliable, F(7,16) = 5.04, p = .004, η_p^2 = .688 (Figure 5.4d). The effect of whether the broken object handle was on the ipsi- or contralesional side varied across patients but was present in all except in one patient (P1).

These analyses indicate that the report of action-related pairs changed as a function of the position of the tool when the tool handle was intact, with performance generally being worse when the tool was on the ipsilesional side relative to when it fell in the contralesional field. This effect of tool position was eliminated when the tool handle was broken. This interpretation is supported by the error data (Figure 5.5, see below).

Error data. The error data from two-item trials when only one item of an object pair was correctly reported were entered into a log-linear analysis, with the factors being handle (intact/broken), side of tool (either on the ipsilesional or contralesional side) and side of reported item (either on the contralesional or on the ipsilesional side). The analysis produced a final model with the highest order interaction (handle x side of tool) and a main effect of reported item, $\chi^2(3)$ = 3.508, p = .320. There was similar performance in reporting ipsilesional and contralesional stimuli (tools, objects), but this held only for the broken tool condition. In contrast, there were more reports of the tool occurring on the ipsilesional than the contralesional side when the tool was intact. Overall, there was better performance in reporting tools compared to objects, and the report was better for ipsilesional compared with contralesional tools (Figure 5.5).

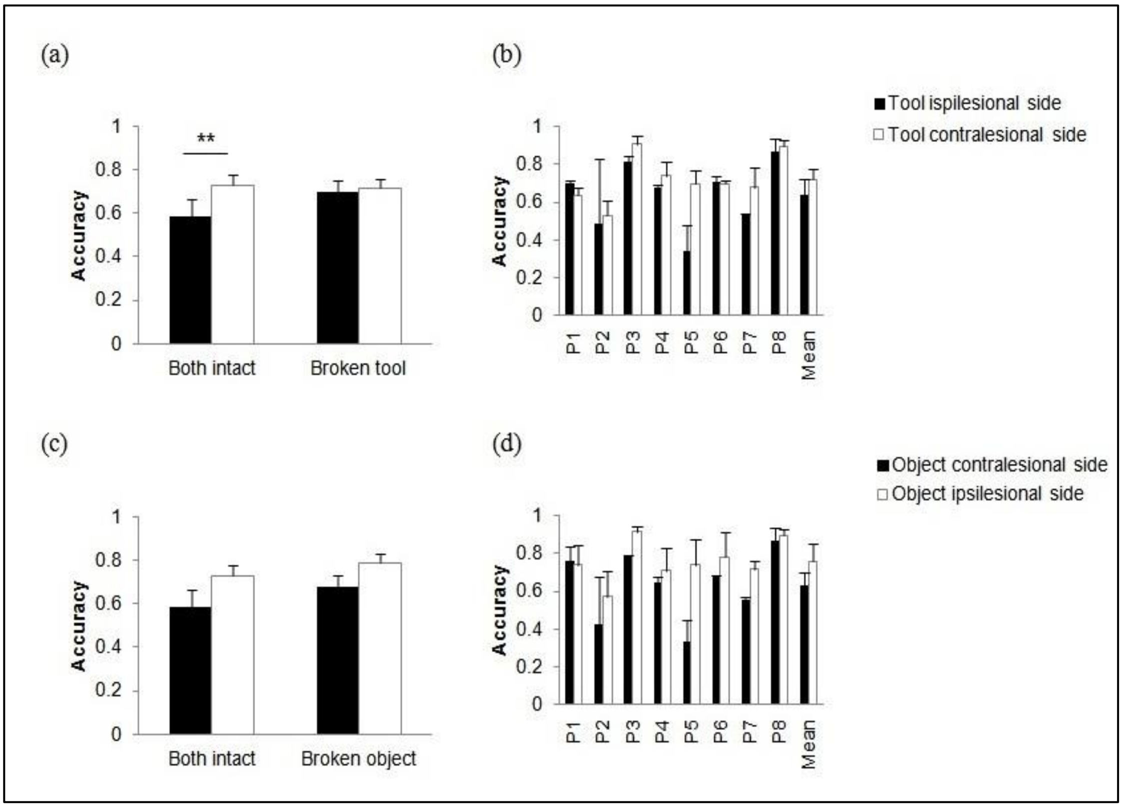

Figure 5.4. Action-related objects only. Effects of breaking the handle of the tool (a, b) or the object (c, d). Mean accuracies for action-related objects as a function of whether the tool handle (a) or the object handle (c) was broken compared to when both handles were intact. Mean patient accuracies (b, d) with error bars denote SE. Asterisks denote significance (**p < .01).

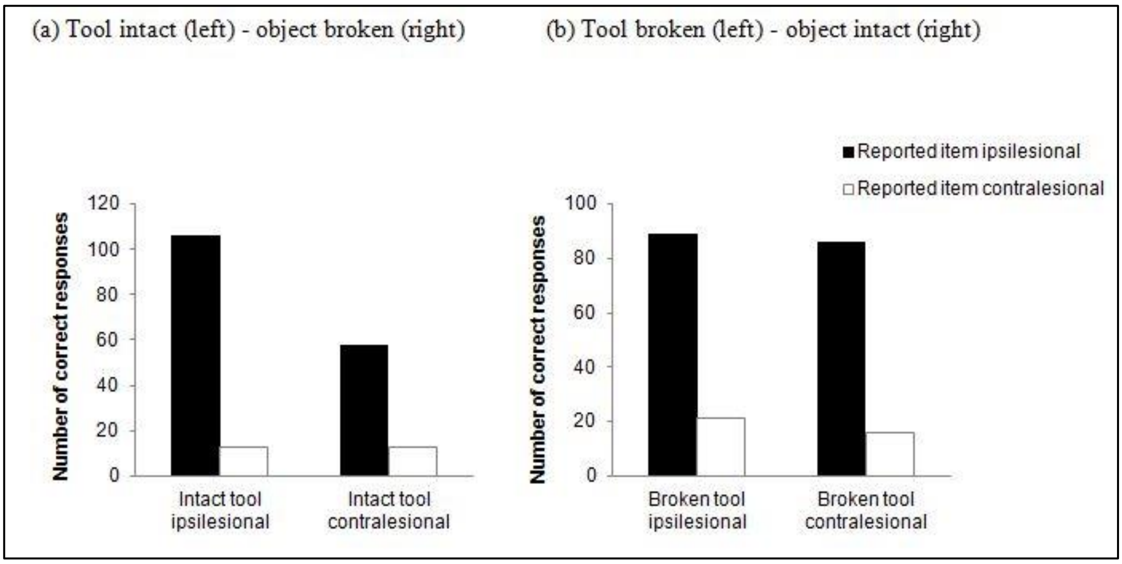

Figure 5.5. Action-related objects only. Number of correct responses for two-item trials when only one item of an object pair was reported (either on the ipsilesional or on the contralesional side) as function of whether the tool handle was intact (a) or broken (b).

(ii) Action-related objects vs. unrelated tools (with broken tool handle; Figure 5.1a (i) vs. Figure 5.1b (i))

The within-subject factors were condition (action-related objects vs. unrelated tools) and location of the broken tool (contralesional vs. ipsilesional field). Patient was treated as a between-subject factor. The only reliable effects were the main effect of patient, $F(7,16) = 9.57$, $p < .001$, $\eta_p^2 = .807$, and the interaction between condition and patient, $F(7,16) = 6.96$, $p = .001$, $\eta_p^2 = .753$. The difference in overall report between action-related pairs and tool pairs varied unsystematically across patients (Figure 5.6). The effects of breaking the handle of the tool were the same for action-related pairs and unrelated tools, consistent with the effect of breaking the handle being largely driven by the tool, in action-related pairs.

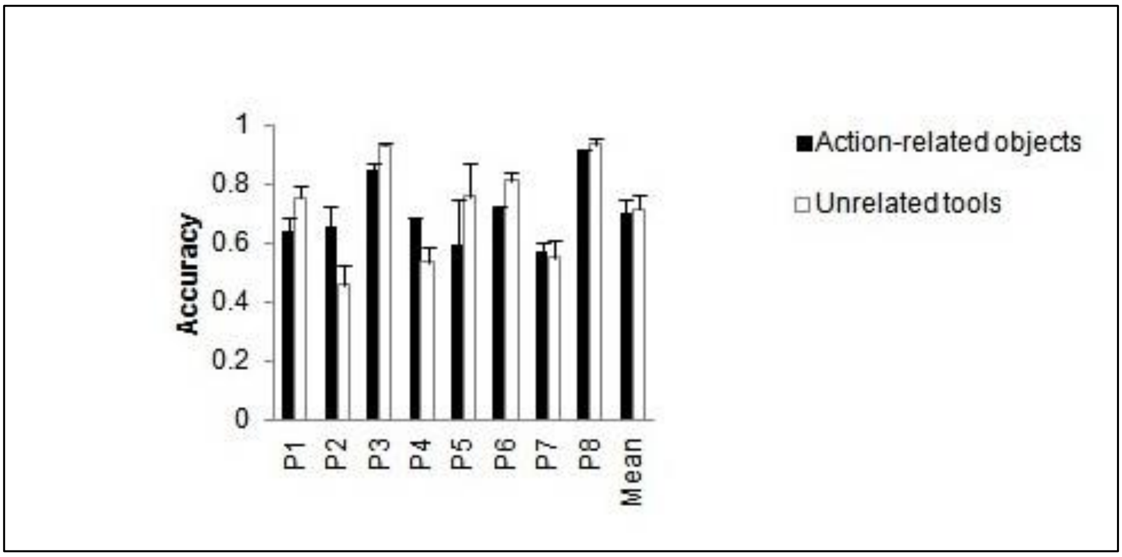

Figure 5.6. Action-related objects vs. unrelated tools, with a broken tool handle. Mean patient accuracies as a function of the pair condition, averaged across the side of the broken tool. Error bars denote SE.

(iii) Action-related objects vs. unrelated objects (with broken object handle; Figure 5.1a (i) vs. Figure 5.1c (i))

The within-subject factors were condition (action-related objects vs. unrelated objects) and location of the broken object (contralesional vs. ipsilesional). Patient was treated as a between-subject factor. The main effects of condition, F(1,16) = 133.36, $p < .001$, $\eta_p^2 = .893$ (action-related objects > unrelated objects), side of broken object, F(1,16) = 9.22, p = .008, $\eta_p^2 = .365$ (ipsilesional > contralesional stimuli), and patient, F(7,16) = 3.77, p = .013, $\eta_p^2 = .623$, were reliable. There was a significant interaction between condition and side of broken object, F(1,16) = 12.46, p = .003, $\eta_p^2 = .438$ (Figure 5.7a). In the action-related condition, performance was increased when the broken object was on the ipsilesional side and the intact tool was on the contralesional side compared to when the stimuli were in the opposite positions, *t*(23) = 3.14, p = .005. In contrast, there was no reliable effect of the side of the broken object with unrelated object pairs. There were also interactions between condition and patient, F(7,16) = 7.57, $p < .001$, $\eta_p^2 = .768$ (Figure 5.7b), and side of broken object and patient, F(7,16) = 2.63, p = .051, η_p^2 = .535 (Figure 5.7c). There was an overall advantage for action-related pairs over unrelated object pairs and for intact tools/broken object handles on the contralesional compared with the ipsilesional side, but these effects varied in size although in the same direction across patients.

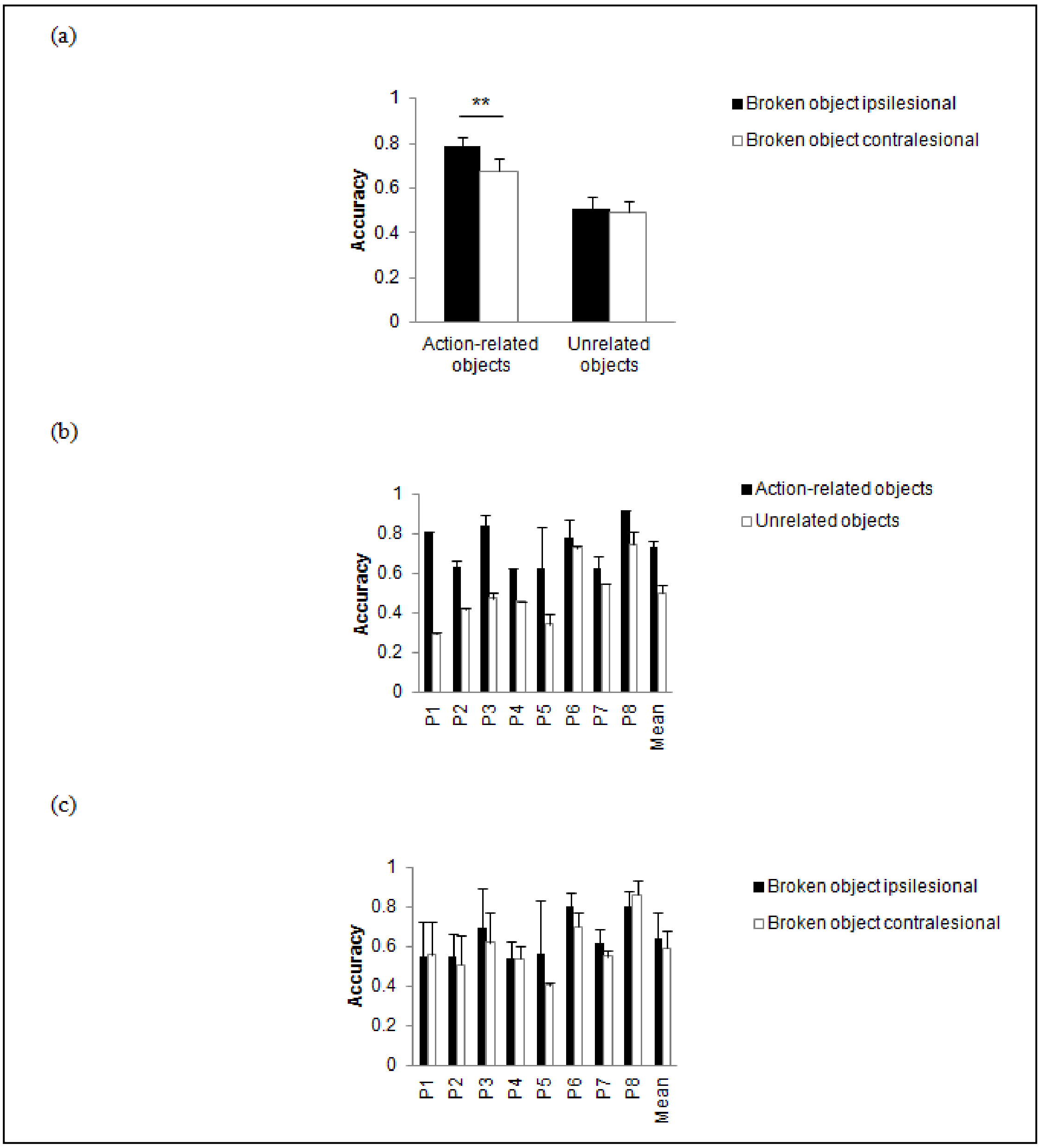

Figure 5.7 Action-related objects vs. unrelated objects, with a broken object handle. (a) Mean accuracy of performance for action-related and unrelated object pairs as function of whether the broken object handle was on the contralesional or on the ipsilesional side. (b) Mean patient accuracies as function of condition (b) and side of broken object (c) with error bars indicating SE. Asterisks denote significance (** $p < .01$).

5.4.4 Effect of stimulus type on one-item report

The accuracy data from unilateral trials were also analysed in order to assess whether there were any differences between the report of tools and other objects when presented in isolation (equivalent to the active and passive members within an object pair; see Methods). The within-subject factors were stimulus type (object, tool), side of stimulus (contra- vs. ipsilesional) and handle (broken, intact); patient was treated as a between-subject factor. There were significant main effects of stimulus type, $F(1,16) = 24.44$, $p < .001$, $\eta_p^2 = .604$ (tools > objects), side of stimulus, $F(1,16) = 38.92$, $p < .001$, $\eta_p^2 = .709$ (ipsilesional > contralesional stimuli), and patient, $F(7,16) = 4.67$, $p = .005$, $\eta_p^2 = .671$. There was also an interaction between stimulus type and side of stimulus, $F(1,16) = 6.35$, $p = .023$, $\eta_p^2 = .284$. Patients tended to report more stimuli on the ipsilesional than the contralesional side (tools, $t(23) = 4.17$, $p < .001$; objects, $t(23) = 3.77$, $p = .001$ (Figure 5.8a). In addition, the interaction between side of stimulus and patient was also significant, $F(6,16) = 5.09$, $p = .003$, $\eta_p^2 = .690$ (Figure 5.8b); patients varied in the magnitude of the side effect but they all showed the same direction. This analysis indicates that the effect of having a broken handle had little effect when single objects were presented (i.e., when there was no spatial competition for selection).

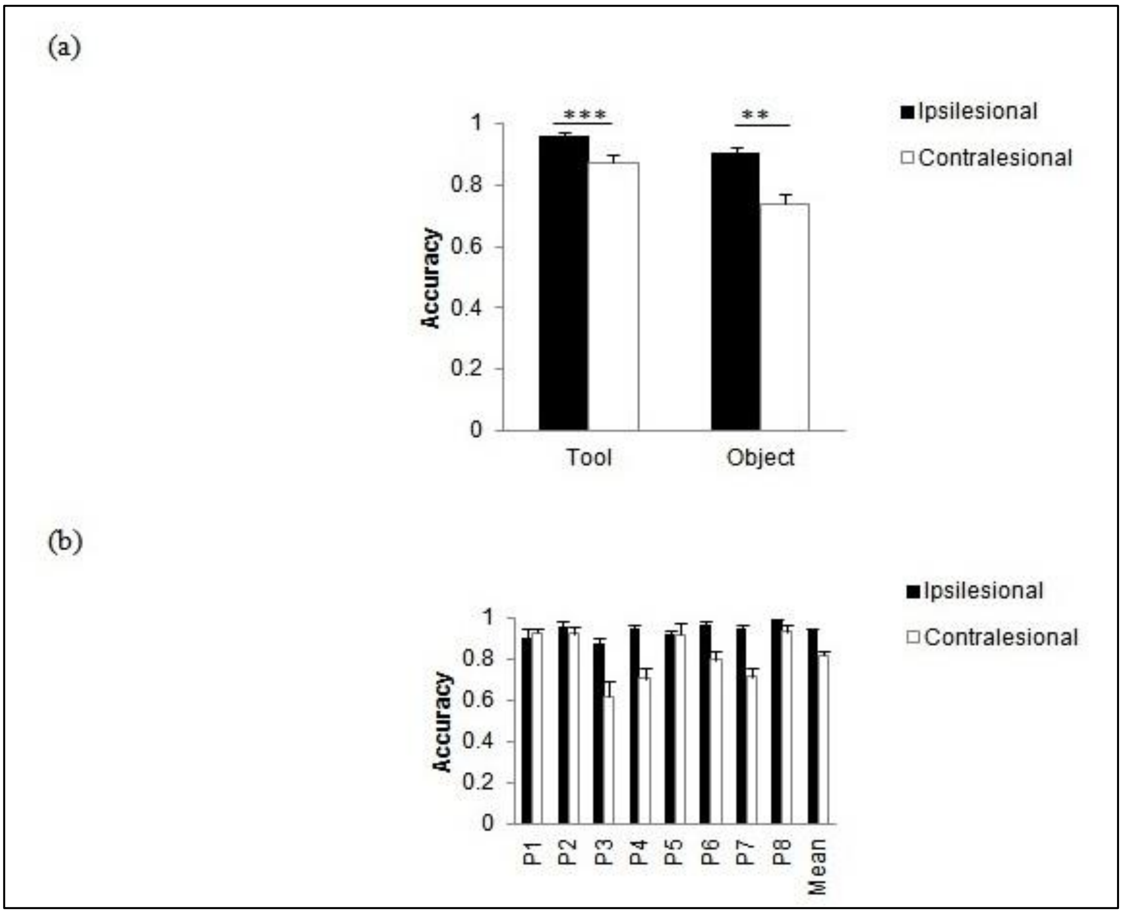

Figure 5.8 The relation between stimulus type (tool, object) and side of stimulus (contralesional, ipsilesional) on unilateral trials. Mean accuracy (a) and mean patient accuracies (b) as function of side of stimulus. Error bars denote SE. Asterisks denote significance (*** p < .001, ** p < .01).

5.5 Discussion

It is well-established that positioning familiar objects for action promotes recovery from visual extinction (Riddoch et al., 2003). Similarly, extinction can be affected by the position of the action-related part of a single object (di Pellegrino et al., 2005). Also, within pairs of action-related objects, attention tends to be drawn to the object that would be grasped to perform the action (the active tool), rather than the passive object (Riddoch et al., 2003). These effects have been attributed to the affordance offered by the objects, which helps to draw attention to the contralesional side (for recent reviews, see Humphreys et al., 2013;

Humphreys et al., 2010b) and to the active object in a pair (Roberts & Humphreys, 2010b). The present chapter investigated whether recovery from extinction held on trials when the affordance was disrupted by presenting objects with a broken handle, and whether the presence of the broken handle altered any bias to attend to the active object in a pair. There were several effects to note, some of which did not relate to the presence of a broken handle and some of which did.

5.5.1 Effects independent of the broken handle

We will initially consider effects that were assessed independent of the presence of a broken handle. Firstly, there was an overall effect of extinction. Patients were able to report more items on one-item trials than on two-item trials. Secondly, patients did benefit overall more when action-related (object-tool) stimuli were presented relative to when unrelated object-object pairs were presented. This is in line with previous studies showing that extinction patients are better at attending to object pairs which have the potential to interact with each other (object-tool pairs here) compared to when this is unlikely (with unrelated objects; e.g., Wulff & Humphreys, 2013; Riddoch et al., 2006). Interestingly, there was no advantage for action-related (object-tool) pairs compared to when two tools were presented. Contrary to our expectation, however, it might be that the two tools themselves afforded a common action together, even though they were unfamiliar as a pair. Familiarity does not appear to be critical here. This interpretation matches the results from the error trials, where only one item of the object pair was reported. There was better report of ipsilesional items for unrelated objects compared to ipsilesional stimuli presented with action-related and unrelated tool pairs. Based on this result, we cannot exclude the possibility that the presence of a tool rather than its relationship to the other non-tool object in a pair is what matters for the affordance effect. This argument seems plausible as the error data revealed that patients overall reported tools over objects (Figure 5.5). In addition, with intact handles, performance was better when the tool was on the contralesional relative to the ipsilesional side (Figure 5.4a). We speculate that either that the presence of the tool helped to cue attention to the contralesional field (cf. di Pellegrino et al., 2005) or that presenting the tool on the ipsilesional side tended to attract attention and led to attentional capture, ipsilesional, and thus increased extinction (e.g., Shalev & Humphreys, 2000). We consider this further below.

5.5.2 Effects when a handle was broken

When the handle of one of the objects was broken, some of the results changed. Notably, when the tool handle was broken, there was now no longer an effect of the position of the tool for action-related objects (Figure 5.4a). The direction of this effect was that performance improved relative to when the tool handle was intact and when the tool fell on the ipsilesional side (Figure 5.4a). This is consistent with an account of attentional capture by an ipsilesional tool with an intact handle – reducing this capture by breaking the handle of the ipsilesional tool led to better report of both items (see above). This argument about attentional capture fits well with the results from the error analysis. Here we observed that patients reported more ipsilesional tools, regardless of whether the tool was broken or not (Figure 5.5).

When the handle of the object (rather than of the tool) was broken, there was no interaction with whether action-related objects or unrelated objects were presented, and the advantage for action-related (object-tool) pairs was maintained (Figure 5.7a). This suggests that breaking the handle of the object has a weaker effect on any affordance-based response to the stimuli, so that the effect of action relatedness is maintained even when a handle is broken. There were also effects of whether the broken handled object appeared on the contralesional or ipsilesional side (better report when it fell on the ipsilesional side, in action-related pairs; Figure 5.4c). However, this result can also be explained in terms of the location of the intact tool, which fell in the contralesional field in the former case (broken handled object in the ipsilesional field). Presenting a tool on the ipsilesional side disrupted performance relative to when the tool fell in the contralesional field, in line with the error analysis (Figure 5.5a).

However, if there was only a detrimental effect of presenting an intact tool on the ipsilesional side, we would not expect to see the overall advantage for action-related objects compared to the unrelated baseline (unrelated tools, unrelated objects) since the tool, in the action-related trials, would disrupt performance. Instead, we suggest that, on top of any attentional capture by the tool, the report of both items was enhanced by coding an action relation between the stimuli, which facilitated attention across both presented items.

Riddoch et al. (2003) and Wulff and Humphreys (2013) both noted that, on trials where patients only reported one item in an interacting pair, the tool was typically identified. Roberts and Humphreys (2010b) also showed that, in normal participants, there is a “prior entry” effect for tools over objects; when the stimuli are presented in co-locations for action, participants tend to identify the tool as appearing before the object (cf. Rorden, Mattingley, Karnath, & Driver, 1997; see also Wulff et al., 2015; Laverick et al., 2015). This is consistent with attention being biased towards the tool (Matheson et al., 2014; Handy et al., 2003). We speculate that, in the present study, this biasing of attention would be exacerbated when the tool falls in the ipsilesional (attended) field and allocating attention to the ipsilesional tool can then disrupt the report of the contralesional object. The interesting result here was that the effect of position of the tool was eliminated when the tool handle was broken but not when the object handle was broken. This observed result for broken tools in our study fits well with the TMS results from healthy participants using single objects. Buccino et al. (2009) presented pictures of intact tools and tools with a broken handle and found that only intact stimuli evoked a motor response. We found a similar pattern with intact paired objects, but not when the handle of one object was broken. This result confirms that viewing non-graspable objects can eliminate motor-based affordance effects. The data further support the assumption that the active tool, rather than the passive recipient of the action has a higher weight within a pair (see e.g., Xu et al., 2015; Wulff & Humphreys, 2013; Riddoch et al., 2003). Taken together, the results indicate that the response to an affordance is modulated by the graspability of the object (the tool in case of action-related object pairs).

In addition to these effects on two-item trials, we found an advantage for reporting single tools over single objects. However, and perhaps in contrast with the study by Buccino et al. (2009), this result was unaffected by whether the tool handle was broken. In the present study, the major constraint on perceptual report was on whether there was competition for attention from an ipsilesional item on the selection of a contralesional stimulus, and this was mediated by whether the tool handle was broken. However, the effects of breaking the handle on attentional competition should be lessened with single objects, as we observed. The data do suggest though that individual items were equally identifiable irrespective of whether or not the handle was broken, and this was not a major factor on report (for a similar result using a spatial stimulus-response compatibility paradigm, see Ambrosecchia, Marino, Gawryszewski, & Riggio, 2015). Thus, the results on two-item trials may more clearly reflect whether tools capture attention, and the effects of attentional capture by tools appear to be lessened when the handle is broken.

Interestingly, there was also a suggestion in the data that the effect of the tool could also have been moderated by the handedness of the patients. P1 and P8 were formerly left-handed. These patients tended to show weaker effects of whether the tool was positioned on the contralesional or ipsilesional side, relative to the other patients (see Figure 5.4b and Figure 5.4d). We may speculate that the drive to attend to the tool when it fell on the ipsilesional side was reduced in these patients, perhaps because it reflects a motor-based response to tools. Since the present patients all had right hemisphere lesions and left-sided extinction, an attentional drive to the right side tool (in the ipsilesional field) would be reduced in the left-handed patients. Clearly, the number of patients here is too small to make strong conclusions, but the effects of handedness on performance remain an interesting question to examine.

A final point to note is that the present result appears to be driven largely by whether an intact tool falls on the ipsilesional side, and attentional capture by this item is moderated by whether the handle is broken. The evidence is consistent with the affordance from the tools being coded in an attended region of field (on the ipsilesional side), but there is not strong evidence for the tool-related affordance being critical when the tool is in the contralesional field. We conclude that performance here is modulated by two factors: (i) an overall effect of having a tool within an object pair (action-related objects = unrelated tools), (ii) coding an action relation between stimuli (action-related objects > unrelated objects), and (iii) attentional capture by an intact tool on the ipsilesional side (overall report better for tool on the contralesional side vs. tool on the ipsilesional side). Only this attentional capture effect was moderated by breaking the handle of the tool.

The present data may have clinical implications. Attentional capture by the active object in the action (the tool) could be used to improve patients' performance in everyday tasks. For example, training everyday tasks such making a sandwich or preparing a hot drink could benefit by always presenting an action pair (e.g., knife and fork) and positioning the tool (the fork) on the contralateral side. Furthermore, our results indicate that drinking containers should have a handle to facilitate affordance perception. Whether patients with other neuropsychological deficits (e.g., apraxia, dementia) would benefit from affordance in a similar way to extinction patients would be an interesting question to follow up.

5.6 Study limitations

We acknowledge that the limited stimulus set could have contributed to these results. The aim of the experiment was to investigate affordance effects with intact and broken objects. As previous studies have shown that the object handle and its orientation is the most prominent feature to guide visual attention (cf. Matheson et al., 2014; Symes et al., 2007), we chose drinking containers with handles to manipulate affordances (cf. Ambrosecchia et al., 2015; Garrido-Vasquez & Schuboe, 2014; Buccino et al., 2009). In order to prevent guessing, we chose distinct drinking containers instead of using different cups or teapots. We do agree that the action pairs "cup-teapot" and "flask-beaker" have a stronger association than non-action pairs (cup-beaker or teapot-flask). We expected that action pairs, in contrast to unrelated pairs, would increase affordance-based responses. Furthermore, we chose highly familiar objects to avoid training effects. We did not observe any improvements across sessions as we adjusted the stimulus exposure time for each session to ensure a similar performance across sessions.

5.7 Conclusion

The present chapter explored whether recovery from extinction was influenced by the graspability of the tool or the passive object within an object pair. The results demonstrate that breaking the handle of the tool rather than of the passive object is crucial for the affordance effect, and thus recovery from extinction. The data further suggest that tools capture attention, with the attentional capture being lessened when the tool handle is broken. In addition, recovery from extinction was higher for both action-related object pairs and unrelated tool pairs compared to unrelated object pairs. This indicates that the potential for action rather than the familiarity with the action pair is important for the perception of affordance (cf. Riddoch et al., 2006).

CHAPTER 6: EFFECTS OF PAIRED-OBJECT AFFORDANCE IN SEARCH TASKS ACROSS THE ADULT LIFESPAN[1]

6.1 Abstract

The present chapter directly examined the role of task relevance and context on the automatic perception of paired-object affordance effects. Specifically, the processes underlying the retrieval of action information about functional object pairs, focusing on the contribution of procedural and semantic knowledge, was investigated. The contribution of procedural knowledge was examined by the way objects were selected, specifically whether active objects were selected before passive objects. The contribution of semantic knowledge was examined by manipulating the relation between targets and distracters. A touchscreen-based search task was used testing young, middle-aged and elderly participants. Participants had to select by touching two targets among distracters using two search tasks. In the explicit action search task, participants had to select two objects which afforded a mutual action (e.g., functional pair: hammer-nail). Implicit affordance perception was tested using a visual-colour matching search task; participants had to select two objects which had the same coloured frame. In both tasks, half of the coloured targets also afforded an action. Overall, middle-aged participants performed better than young and elderly participants, specifically in the action task. Across participants, in the action task, accuracy was increased when the distracters were semantically unrelated to the functional pair, while the opposite pattern was observed in the colour task. This effect was enhanced with increased age. In the action task, all participants

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[1] Chapter 6 is an adapted version of Wulff, M., Stainton, A., & Rotshtein, P. (submitted). Effects of paired-object affordance in search tasks across the adult lifespan. *Brain and Cognition.*

utilised procedural knowledge, i.e., selected the active object before the passive object. This result supports the dual-route account from vision to action. Semantic knowledge contributed to both the action and the colour task, but procedural knowledge associated with the direct route was primarily retrieved when the task was action-relevant. Across the adulthood lifespan, the data show inverted U-shaped effects of age on the retrieval of action knowledge. Age also linearly increased the involvement of the indirect (semantic) route and the integration of information of the direct and the indirect routes in selection processes.

6.2 Introduction

The processing of visual scenes is influenced by many factors. Gibson (1979) first outlined the concept of affordance, proposing that objects are not only perceived in terms of their visual properties but also in terms of what they afford (e.g., a knife affords cutting). Several studies have demonstrated that affordance processes are activated automatically when we view an object, regardless of the viewer’s intention to act upon it (e.g., Grezes & Decety, 2002). Affordance effects can also be observed when two objects engage in a functional interaction: one object acting upon the other to produce an action (a bottle pouring into a glass; Gibson, 1979). Accumulating evidence demonstrates that attention and perception is facilitated when a functional relation between objects exists (e.g., Wulff et al., 2015; Laverick et al., 2015; Xu et al., 2015; Wulff & Humphreys, 2015, 2013; Borghi et al., 2012; Roberts & Humphreys, 2011a; Green & Hummel, 2006; Riddoch et al., 2003). It has been argued that affordance facilitates perception through the direct route from vision to action without accessing semantic knowledge. However, the interplay between procedural and semantic knowledge when retrieving action knowledge is still debated. In the present chapter, we examined the contribution of procedural and semantic knowledge to action retrieval using two different search tasks. We also explored whether this interaction would change across the adulthood lifespan.

The dual-route account from vision to action (Riddoch et al., 1989) assumes that action retrieval is mediated by two routes: A direct route based on the structural properties of objects (affordances) which automatically activates action and motor procedures (i.e., procedural knowledge; e.g., how to grasp a knife and how to use a knife with a fork) by-passing semantic knowledge. The direct route is assumed to be mediated by the dorsal (occipito-parietal) visual pathway mediating object-related actions (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). The dorsal visual stream route has been further subdivided into a dorso-dorsal and a ventro-dorsal stream (Rizzolatti & Matelli, 2003). The dorso-dorsal stream connects area V6 with areas V6A and MIP of the superior parietal lobule, while the ventro-dorsal stream connects the inferior parietal lobule with superior medial temporal (MT/MST) and ventral pre-motor cortices (Rizzolatti & Matelli, 2003). It is assumed that the link between affordance perception and motor procedures depicting the way we interact with objects is mediated by the ventro-dorsal stream rather than the dorso-dorsal stream associated with the on-line control of action (Binkofski & Buxbaum, 2013; Buxbaum & Kalenine, 2010; Rizzolatti & Matelli, 2003). A second indirect route enables retrieval of semantic knowledge by accessing previous knowledge about the object (e.g., knowledge on when and what is a knife used for). This knowledge is stored as part of the semantic memory system (e.g., a knife as many other kitchen items is used in the context of food such as eating, preparing etc.; for a simulation of the dual-route model, see Yoon et al., 2002). The indirect semantic route is associated with the ventral (occipito-temporal) visual pathway for recognizing objects (Goodale & Milner,

1992) which terminates in the anterior temporal lobe where conceptual knowledge is believed to be represented.

The hypothesis that action retrieval can be mediated by the direct route from vision to action is supported by neuropsychological data (for a review, see Humphreys & Riddoch, 2003). For example, patients with left occipito-temporal brain damage were able to make appropriate gestures to objects even though they were unable to name the objects (e.g., Yoon, Humphreys, & Riddoch, 2005; Riddoch and Humphreys, 1987; for a similar dissociation in semantic dementia patients, see Hodges et al., 2000; Hodges, Spatt, & Patterson, 1999). The opposite pattern is evident for patients with left parietal brain damage. These patients were able to access semantic knowledge but they were impaired when asked to interact with objects (Riddoch et al., 1989). This double dissociation confirms the existence of a direct route and challenges the traditional view that vision to action interacts only indirectly through semantic knowledge (Ochipa et al., 1992).

Even though the above cited literature supports the direct route for procedural knowledge retrieval and the indirect route for semantic knowledge retrieval, there is evidence that the direct and the indirect route may both contribute to action retrieval. For example, using computational modelling (naming and action model; Yoon et al., 2002), it has been shown that damage to one route impaired ("blocked") action retrieval of the other route. This is supported by experimental data showing a strong linear relationship between semantic impairment and accuracy of object use (Silveri & Ciccarelli, 2009), specifically when using the same stimulus set in semantic dementia patients (Hodges et al., 2000). Neuroimaging evidence in healthy participants also suggests a link between action and semantic knowledge. For example, Mizelle et al. (2013) showed that the indirect (semantic) route was involved in evaluating functional relations between objects, and thus linking action semantic and action procedural systems. Taken together, these above cited studies suggest a strong relationship between action and semantic knowledge (see also, Frey, 2007; Bozeat et al., 2002; Buxbaum et al., 1997).

There is growing evidence that the interaction between the direct (affordance) route and the indirect semantic route also affects selection processes. Patients with right fronto-parietal brain damage and left-sided extinction, a disorder of spatial selective attention, were able to report more objects in their extinguished hemifield when the objects were presented in a way that afforded an action (a fork and knife facing each other) or not (a knife facing away from a fork; Wulff & Humphreys, 2013; Humphreys et al., 2010a; Riddoch et al., 2006; Riddoch et al., 2003). Note that mere semantic associations between objects did not facilitate selective attention processes in these patients (Riddoch et al., 2003; for a similar result with healthy participants, see Adamo & Ferber, 2009). Similarly, healthy participants showed improved performance when the objects were functionally related compared to when they were unrelated (McNair & Harris, 2014; Borghi et al., 2012; Roberts & Humphreys, 2011a; Adamo & Ferber, 2009; Green & Hummel, 2006).

An important action cue for interacting objects is the functional role of each object within an action pair (i.e., procedural knowledge). Riddoch et al. (2003) differentiated between the active and the passive object within a pair, with the active object (e.g., bottle) being the one which is typically gripped by the dominant hand and acts upon the passive object (e.g., glass) gripped by the non-dominant hand to produce the action (cf. Laverick et al., 2015). However, which hand is used to grasp the active object is influenced by the context in which the objects will be used (e.g., drinking vs. pouring). Studies with healthy participants also demonstrated an attentional bias toward the active object (Wulff et al., 2015; Laverick et al., 2015; McNair & Harris, 2014; Roberts & Humphreys, 2010b; Tipper et al., 2006). McNair and Harris

(2014), for example, manipulated the temporal sequence of a tool (the active object) or its corresponding action recipient (the passive object) in an attentional blink paradigm. Reduced attentional blink occurred when the active object preceded the passive object but not when the temporal order was reversed. These results suggest that the tool (i.e., the active object) has a higher attentional weight than its action recipient (i.e., passive object) in an action pair.

Wulff and colleagues (Wulff et al., 2015; Laverick et al., 2015) investigated the contribution of semantic and procedural knowledge to the retrieval of action knowledge by manipulating these two factors orthogonally using real objects and static pictures of the same objects on a screen. In the real object task, participants performed a conceptual search, i.e., they had to select a pair of real objects affording a mutual action among distracters. In this task, search targets were identified based on the retrieval of action knowledge. The authors assessed the involvement of semantic processes in action decisions by manipulating the semantic relation between action pair and distracters. For example, for the action pair knife and fork, the semantically related distracters were cup and spatula and the unrelated distracters were pen and scissors (kitchen vs. office items, respectively). Procedural knowledge was assessed using the way/order objects were selected. Specifically, if objects were selected in a manner matching the execution of an action (e.g., selecting the active object first with the right hand) this would indicate an involvement of the direct (procedural) route in the retrieval of action knowledge. In the computerised version of the experiment, participants had to decide by button press whether two consecutively presented objects can interact with each other. Here the involvement of semantic knowledge was assessed by the time to reject a functional relation between two semantically related or unrelated objects. As with real objects, the involvement of procedural knowledge was tested by manipulating the order by which the active and passive objects were presented and the way objects were gripped. Facilitation of action decisions for active-before-passive objects or congruently gripped objects for action would indicate the involvement of procedural knowledge.

In both studies (Wulff et al., 2015; Laverick et al., 2015), semantically related distracters interfered with making action decisions in the computer task, whereas the effect of semantic interference was attenuated with real objects and only observable when the selection was made with one hand (Wulff et al., 2015) but not when the selection was made bi-manual (Laverick et al., 2015). In both studies, procedural knowledge affected selection processes. Specifically, with real objects the active object within an action pair was selected first (Wulff et al., 2015; Laverick et al., 2015), primarily with the right hand (Laverick et al., 2015). Similar results were observed in the computerised version of the experiment; action decisions were facilitated when the objects were congruently gripped and when the active object was presented before the passive object. We tested healthy young and elderly participants, with both age groups showing a similar performance pattern (Laverick et al., 2015).

Using the above-described paradigms, we studied the neurocognitive the mechanisms underlying selecting objects for action in neuropsychological patients (Wulff et al., 2015). Based on the accuracy performance in the real object task, patients were classified as intact or as impaired compared to the accuracy performance of healthy age-matched controls. Impaired patients in contrast to intact patients were poorer when selecting objects for action among distracters, with similar interference from semantically related and unrelated distracters. In the computerised version, impaired patients also performed poorer than intact patients, although the effects of procedural and semantic knowledge were weakened. Across both tasks, there was evidence that impaired patients were able to utilise to some extent procedural knowledge (active before passive object; congruent hand grip information). We suggested that impaired patients had degraded access to both procedural and semantic knowledge. This has been supported by a subsequent lesion subtraction analysis. At the group level, impaired patients compared to intact patients had lesions to the dorsal (pre-motor and inferior parietal cortices) and the ventral (anterior temporal cortices) visual stream. The former has been associated with the processing of object-directed actions, while the latter is assumed to be involved in object recognition (Goodale & Milner, 1992). Thus, the ability to select objects for action relies on access to both procedural and semantic knowledge.

Taken together, the data of Wulff and colleagues (Wulff et al., 2015; Laverick et al., 2015) support the notion that the retrieval of action knowledge results from the interaction between the direct procedural (probably ventro-dorsal) and the indirect semantic (ventral) routes. However, these two studies have several limitations. Firstly, in the computerized version of the experiment the stimuli were presented sequentially and thus evoked working memory processes in order to make action relation decisions on any of the two sequentially presented objects, while the experiment with real objects where all objects were presented at the same time instead evoked selection processes. Secondly, both studies only focused on the explicit retrieval of action knowledge. Thus, it is still unclear whether procedural knowledge will be ‘automatically’ activated even when the task is action-unrelated. Furthermore, the effect of age on the retrieval of action knowledge still remains open, as the sample sizes were relatively small (Laverick et al., 2015) or there was no direct comparison between different age groups (Wulff et al., 2015).

Does the involvement of the direct route in selecting objects for action depend upon task demands, i.e., the observer’s intentions?. Gibson (1979) argued that the affordance properties of objects are perceived automatically. It is unclear whether the affordance for paired objects is also automatically perceived or whether it depends upon experience, and some learned knowledge of object properties in different action contexts, and thus on long-term stored action knowledge. Action knowledge can be represented in two forms: A screwdriver and a screw can be represented through the way of how they can be used together (procedural knowledge), or through the knowledge that a screwdriver is typically used together with a screw (semantic knowledge). Yoon and Humphreys (2007), for example, showed that the manipulation of affordance procedural cues (i.e., object orientation) affected action decisions but not semantic decisions. In another study, Yoon and Humphreys (2005) demonstrated that hand grip and hand movement information primarily affected action decisions, with the effect being diminished when the task required object naming. Furthermore, action but not semantic decisions were facilitated when pairs of objects afforded an action and when the objects were aligned with the preferred hand position of the participant (Yoon et al., 2010). On the other hand, Borghi et al. (2012) reported that relation decisions were facilitated for functionally related objects relative to when the objects were spatially related, with the effect being magnified when the objects were gripped for action. Similarly, target identification based on a verbal probe was facilitated when the target object was presented in the context of a functionally related distracter and when the two objects were oriented for an action (Green & Hummel, 2006). In sum, action procedural information in the stimuli facilitates action-related decisions but there is also evidence that action information contributes to semantic decisions.

Whether affordance processes are modulated by age has not been examined; nor is it clear whether the ability to select objects for action remains stable over the lifespan. In general, there are two different models of how cognition might change across the lifespan. One possibility is that performance across the lifespan changes nonlinearly (e.g., Potter, Grealy, Elliott, & Andres, 2012; Waszak, Schneider, Li, & Hommel, 2009; Hommel, Li, & Li, 2004). For example, Potter et al. (2012) asked young, middle-aged and older participants to search for a specific jar of pasta among other jars of pasta with different shapes and colours. The authors reported non-parametric age-related decline in search performance, with age-related decline evident from middle-aged adults onwards. A similar pattern was found using visual masking (Waszak et al., 2009) and emotion recognition (Horning, Cornwell, & Davis, 2012). In the context of action knowledge (e.g., tool innovation and creativity), research has revealed a potential inverted U-shaped performance, with middle-aged participants showing superior performance compared to younger participants (Reese, Lee, Cohen, & Pucket, 2001). On the other hand, it has been suggested that performance deteriorates linearly throughout the adulthood lifespan (Salthouse, 2000). Note that these studies often only focused on the extreme ends or tails of the lifespan distribution (young vs. old). Several studies comparing young and elderly adults show that age affects selective attention. For example, elders have a weak representation of the target object combined with a decreased ability to ignore distracters (e.g., Tsvetanov, Mevorach, Allen, & Humphreys, 2013; Kok, 2000; Rogers, 1992). In these above-cited studies, selection was guided by bottom-up processes (potentially relying on fluid intelligence); it is therefore unclear whether conceptual selection based on long-term knowledge/experience (potentially relying on crystallised intelligence) would be also affected by age. There is evidence that crystallised intelligence (e.g., conceptual knowledge, skills, experience) improves or remains stable over the lifespan, whereas fluid intelligence (e.g., attention, processing speed, cognitive control) declines with age (for a review, see Craik & Bialystok, 2006). In the absence of studies testing middle-aged participants, it is unclear how the different types of selection processes are manifested in middle-aged adults.

Age-related changes have been also reported for tool-related knowledge (for a recent review, see Mizelle & Wheaton, 2010a). Ska and Nespoulous (1987), for example, showed that elders pantomime the use of a tool in a qualitatively different way than young participants. Elders focused on the movement of the tool and substituted the missing object with their body (e.g., using a fist to represent the hammer head) – potentially stressing the outcome (semantic knowledge) of what the tool is used for, while young participants focused on the hand-object interaction (e.g., pretending to hold the hammer handle; see also, Rodrigues & Caramelli, 2009) – emphasising procedural knowledge of how the tool is used. Moreover, it has been shown that elders were poorer at predicting the time course of familiar actions compare to young participants (Diersch, Cross, Stadler, Schutz-Bosbach, & Rieger, 2012). These findings suggest some changes in the way action knowledge is retrieved, with elderly participants focusing on semantic knowledge (‘what for’) and young participants on procedural knowledge (‘how to’). As mentioned above, the lack of age-related effects in our previous studies (Wulff et al., 2015; Laverick et al., 2015) might be related to the relatively small sample size and the relatively low number of trials in the conceptual (real object) search task. These factors might have reduced statistical power by increasing noise. There are hardly any studies which investigate the retrieval of action knowledge in middle-aged adults. Thus, it remains open whether there would be age-related differences across the lifespan in utilising action knowledge when making action and non-action decisions.

The present chapter further examined the contribution of procedural (direct route) and semantic (indirect route) knowledge to the retrieval of action knowledge as manifested by paired-object affordance in the context of selection processes. Extending our previous work (Wulff et al., 2015; Laverick et al., 2015), we investigated the impact of task relevance and age on selection processes. Specifically, to examine the effects of task relevance, we used two search tasks. One task required explicitly to retrieve action knowledge (‘select the two objects that typically interact to perform an action’; action task). This was a conceptual search task as the targets were identified based on prior knowledge. The second task assessed the implicit processing associated with action knowledge. Here participants had to select two objects that had the same coloured frame (colour task). This was a visual-based search task as targets were identified based on the visual properties of the items. We also controlled for the congruence of cues (targets' action relation and frame colour) in the search array, with half the trials providing congruent action-colour cues (functional pair had the same coloured frame) and the other half incongruent action-colour cues. Importantly, identical displays (stimuli, search arrays etc.) were used in both search tasks, and hence any observed effects can only be attributed to the specific task demands. We note that in the context of the colour task, the assessment of the processes contributing to implicit retrieval of action knowledge was only meaningful in congruent trials, i.e., when the coloured-framed targets were also functionally related (as in the action task), but this information was irrelevant to the task.

As in our previous studies (see above), we assessed the contribution of procedural and semantic knowledge orthogonally. The involvement of the semantic route in the selection process was assessed by manipulating the relation between targets and distracters. The distracters were semantically related to the targets (e.g., both targets and distracters are used in grooming or in bathroom) or unrelated (e.g., targets are used for food preparation but distracters are used for grooming). Based on previous research, we predicted that semantically related relative to unrelated distracters will interfere more during the explicit retrieval of action knowledge, namely when selecting objects for action.

The involvement of procedural knowledge in selection processes was assessed by recording how objects were selected. Within each functional pair, we defined the active and the passive object. It has been shown that the active object is selected first especially when the selection is made with the dominant hand (Laverick et al., 2015). We anticipated that the active object would be selected before the passive object in the action task, an effect which may be emphasised if the active object is in vicinity to the dominant hand. If paired-object affordance cues (i.e., procedural knowledge) are evoked automatically, we also expected to see order selection effects in the colour task, when the coloured targets were functionally related.

As we manipulated and assessed the contribution of semantic and procedural knowledge to action retrieval independently, we could also test whether there was evidence for an interaction between these two knowledge streams. For example, if semantic knowledge contributes to action retrieval, does the impact of procedural knowledge increases when semantic knowledge provides an ambivalent cue e.g., when distracters and targets are semantically related?

Finally, in line with previous research on cognitive ageing, we expected increased contribution of the semantic route to action retrieval with increased age. We also anticipated an overall decline in performance with age in the visual-based (fluid intelligence) but not in the conceptual-based (crystallised intelligence) search task. Though, these hypotheses were speculative due to the paucity of the data, especially on this topic.

6.3 Method

6.3.1 Participants

Forty-five healthy participants, 15 female right-handed undergraduate students (M = 19.00, SD = 0.65, age range: 18-20), 15 middle-aged postgraduate students (7 females, 1 left-handed, M = 38.97, SD = 6.78, age range: 30-51) and 15 elderly participants (5 females, 2 left-handed, M = 72.67, SD = 6.34, age range: 62-93) took part in the study. We recruited participants from three different age groups to generalise results across the lifespan. To provide a better description of our elderly sample, all but one elderly participants were tested with the Oxford Cognitive Screen (Demeyere, Riddoch, Slavkova, Bickerton, & Humphreys, 2015, see Appendix 2 for test scores). One elderly participant was found to be impaired in visuo-spatial skills, scoring below the cut-off with 31 out of 50 correct responses (group average = 44.7). Another elderly participant scored below the cut-off with 2 out of 4 in the number calculation task (group average = 3.5). A third elderly participant scored below the cut-off in the executive function task, making a total of 5 errors (group average = 1.46 errors). Handedness was determined by self-report. Elderly and middle-aged participants were paid for their participation and students were granted course credit. All participants reported normal or corrected-to-normal vision. None of the participants reported a history of neurological or psychiatric impairment. Informed consent was obtained from all participants and the study was approved by the local Ethical Review Committee.

6.3.2 Stimuli and design

Thirty common household objects found in the kitchen, office and garage were used. Each object was photographed in a neutral position against a bright background (600 by 400 pixels in size; see Figure 6.1) with the handle facing towards the observer. This was done to avoid that the objects would afford a particular hand grip and to reduce proximity cues that may be present when the objects are positioned to interact together with each other (e.g., a bottle is tilted towards a glass or a hammer is facing towards the nail). Each picture was presented surrounding by coloured frame of red, blue, green, yellow, or pink. The pictures were edited using GIMP 2.8.14 software.

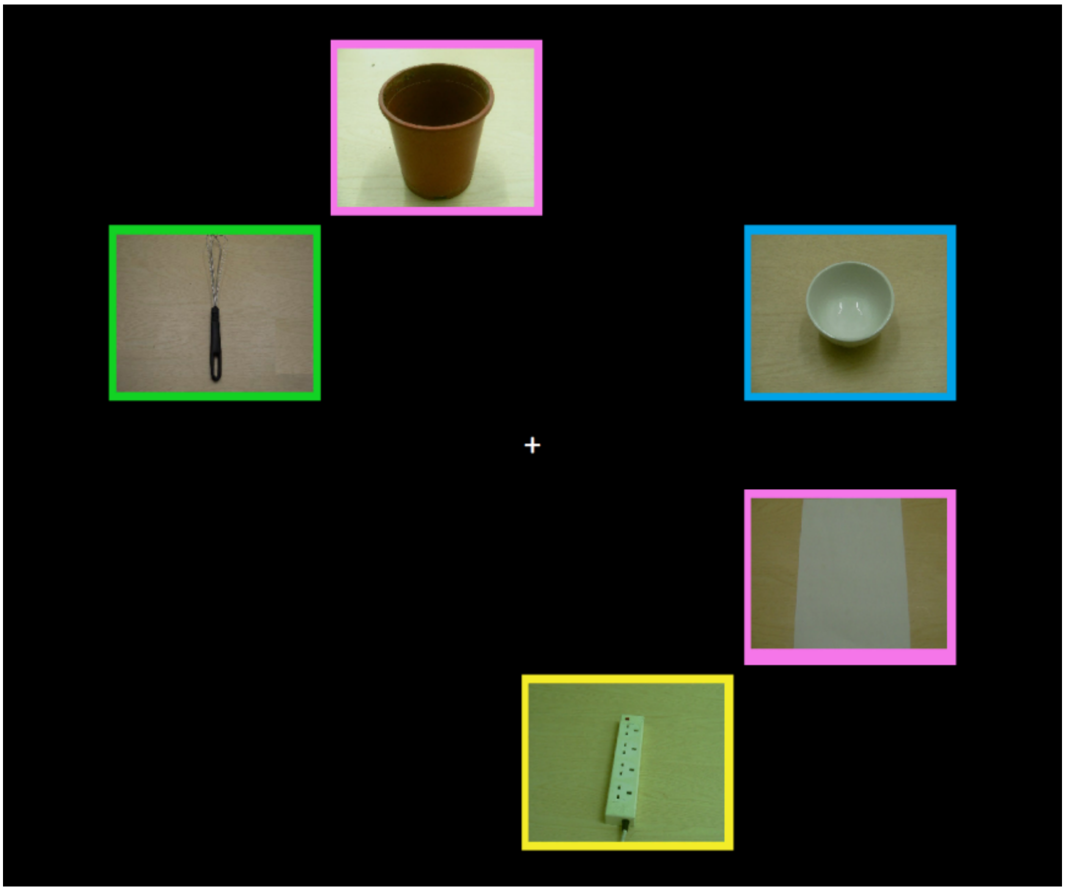


Figure 6.1. Example of an experimental trial for the action task. The target objects were a whisk and a bowl; the unrelated distracters were paper, plant pot and socket. Note that this is an incongruent trial; target objects have a different coloured frame.

A pilot study was conducted to create individual object sets for each trial. In each object set two objects formed an action pair and three were distracters. The aim was to create search array sets which would include a highly familiar functional object pair and distracters which would not afford a mutual action with any of the other items on this display. We aimed to create two search arrays for each action pair, one in which the distracters were semantically related and one in which the distracters were semantically unrelated to the target pair (cf. Table 6.1). Distracters were considered semantically related if they had a meaningful association with the targets such as they can be found in the kitchen but they cannot be conventionally used together in action (Borghi et al., 2012). Using written words, corresponding to the name of objects, twelve participants (10 females, 20-52 years of age) were asked to identify the action pair in each object set. They were then asked if they recognised any other potential action pair(s) within that set. If a set was identified as possessing more than one action pair, the distracters were altered to eliminate any additional action pairs to the target action pair. An iterative procedure was used, meaning that the pilot study was continued until there was a complete agreement across all object sets and across all participants that there was only one clearly identifiable action pair. Another pilot study with seven participants (2 females, 20-52 years of age) was run to validate the active-passive classification within each of the 14 object pairs. See Table 6.1 for a full list of object pairs and the corresponding distracter objects.

Based on the pilot data, the individual objects were combined to make 14 search arrays; each set contained five objects (two target objects and three distracters). The objects were presented at equal distances to the central fixation cross (Figure 6.1). In each trial the two targets appeared to the left and the right side of the fixation cross. However, to reduce the possibility of strategic searching, in 7% of the trials the target objects appeared in the same visual hemifield; these catch trials were analysed separately.

The experiment consisted of two search tasks: an explicit conceptual task (referred to as action task) and an implicit visual-based search task (referred to as colour task). In the action task, participants had to select the two objects that could be used together (i.e., having an action relation or not; explicit retrieval of action knowledge); in the colour task, participants had to select the two objects that had the same coloured frame (implicit retrieval of action knowledge). The same object set was used in both tasks.

Table 6.1 Object pairs used in the study

Active object	**Passive object**	**Semantically related distracters**	**Semantically unrelated distracters**
Bottle opener	Beer bottle	Knife, coffee jar, whisk	Trowel, knife, scoop
Corkscrew	Wine bottle	Teapot, scoop, tin	Paint tin, spoon, screw
Ice cream scoop	Ice cream	Tin opener, spatula, peeler	Screwdriver, frying pan, paper
Knife	Fork	Wine bottle, coffee jar, scoop	Paintbrush, scoop, tin opener
Paintbrush	Paint tin	Trowel, scissors, screwdriver	Fork, teapot, spatula
Peeler	Potato	Mug, tin opener, corkscrew	Beer bottle, plant pot, scoop
Scissors	Paper	Spatula, whisk, tin opener	Bowl, tin opener, frying pan
Screwdriver	Screw	Scissors, whisk, paintbrush	Fork, trowel, coffee jar
Spatula	Frying pan	Peeler, teapot, ice cream	Coffee jar, bottle opener, paint tin
Spoon	Bowl	Peeler, wine bottle, frying pan	Plant pot, paintbrush, peeler
Teapot	Mug	Knife, bottle opener, bowl	Washing up liquid, screwdriver, ice cream
Tin opener	Tin	Peeler, ice cream, coffee jar	Scissors, plant pot, ice cream
Trowel	Plant pot	Paper, screw, paint tin	Tin, scissor, beer bottle
Washing up liquid	Sponge	Potato, wine bottle, coffee jar	Screw, potato, paper

We manipulated four factors: Task (action, colour), Distracter (related, unrelated), Congruence (congruent, incongruent) and Side of Active Object (left, right). In half of the trials the active object appeared on the right side and the passive object on the left side and vice versa. Regardless of the task, trials were considered as congruent when the active and passive object of an action pair had the same coloured frame (congruent action-colour cue), while in incongruent trials the active and the passive object of an action pair did not match in colour (incongruent action-colour cue; Figure 6.1). Note that in the colour task, the targets were functionally related in the congruent condition (i.e., formed an action pair) but they did not form a functional pair in the incongruent condition. In these latter trials, there was always an action pair in the array, either between two distracters or between a target and a distracter.

The congruence manipulation allowed us to examine whether functional relations are processed implicitly though they are task-irrelevant.

The experiment was divided into two runs (448 trials in total). In each run, there was a separate block for each task (224 for each task). Due to time restraints 14 out of 45 participants (2 students, 12 elders) completed only one run of each task (224 trials in total). The pattern of results was not different when we ran the analyses using equal amount of trials (224) for each participant (see Appendix 3 for reliable main effects and interactions of the accuracy data). Hence the findings reported here are based on all the collected data. The order of the task blocks was counterbalanced across participants. Within each task block, object pairs were presented pseudo-randomly. There were 56 trials for each distracter condition. Additionally, there were 64 catch trials in which both objects appeared on the same side.

6.3.3 Procedure

Participants sat within comfortable reaching distance of a touchscreen monitor. The search array contained target objects and distracters and the participants performed either the action or the colour task. In the action task, participants were instructed to touch with their preferred (typically their dominant) hand the two targets which could be used together in action (e.g., knife and fork). In the colour task, participants were asked to touch the two targets with matching coloured frames (e.g., both frames were blue). If participants were unable to find the targets, they were instructed to touch the fixation cross. The stimuli remained on the screen until a response was made. The next trial immediately followed. Prior each task, participants were given at least five practice trials. Participants were instructed to put their hand at the spacebar before selecting the first object to ensure equal distances between left and right targets. RT for the whole trial was defined as the time the second target was touched.

The stimuli were presented on a 22-inch touchscreen monitor with a screen resolution of 1920 x 1080 pixels using E-prime software (Version 2.1; Psychology Software Tools, 2006).

6.3.4 Data analysis

The data analysis was completed using IBM SPSS Statistics 19 (SPSS Inc., Chicago, IL). To assess the contribution of the semantic route to action retrieval as a function of task relevance, we used accuracy and RT data. We standardised the RT data for each participant to account for slowed processing speed associated with increased age. The data were examined with a 2 x 2 x 2 [Task (action, colour) x Distracter (related, unrelated) x Congruence (congruent, incongruent)] repeated-measures ANOVA with Age (young, middle-aged, older) as a between-subject factor. Interaction effects were evaluated with paired *t*-tests ($p \leq .05$).

The contribution of procedural knowledge to action retrieval was assessed using only congruent trials. We computed for each participant and condition the proportion of trials in which the active object was selected before the passive object. In addition, we divided the trials based on the side the active object was presented. We only included right-handed participants (N=40) to ensure that the results were not driven by the hand used; the response pattern was similar when the three left-handed participants were also included.

6.4 Results

One middle-aged and one elderly participant were excluded due to an error rate of more than 30% in the action and/or colour task, indicating that s/he potentially did not understand the task. For the remaining participants (N_{Young}=15, $N_{Middle\text{-}aged}$=14, and $N_{Elderly}$=14), overall accuracy was high 94% (action task: 94%, colour task: 94%), indicating that participants easily found the target objects. The error pattern of catch trial revealed that participants were more surprised when an action pair rather than a colour pair appeared in the same visual hemifield (20% vs. 3%, respectively). The mean accuracies and zRT data for each age group are presented in Appendix 4.

Accuracy. We start by reporting the effects across all participants. The main effect of Task was not reliable, F(1,40) = .464, p = .464, η_p^2 = .013. There were significant main effects of Distracter, F(1,40) = 57.73, p < .001, η_p^2 = .591 (related > unrelated), and Congruence, F(1,40) = 62.78, p < .001, η_p^2 = .611 (congruent > incongruent). The main effects of Distracter and Congruence should be interpreted in line with the observed interactions. Across all participants the task by distracter interaction, F(1,40) = 159.76, p < .001, η_p^2 = .800, the distracter by congruence interaction, F(1,40) = 11.79, p = .001, η_p^2 = .228, as well as the interaction between these three factors (Task x Distracter x Congruence), F(1,40) = 85.29, p < .001, η_p^2 = .681, were reliable (Figure 6.2). This latter interaction was decomposed by conducting separate 2 x 2 ANOVAs for each task collapsing across age groups.

For the *action* task, there were significant main effects of Distracter, F(1,42) = 11.64, p = .001, η_p^2 = .217 (unrelated > related), and Congruence, F(1,42) = 20.85, p < .001, η_p^2 = .332 (congruent > incongruent). Responses were more accurate when the two action targets had the same coloured frame and when the search array contained semantically unrelated distracters. There was also a reliable interaction between distracter and congruence, F(1,42) = 9.35, p = .004, η_p^2 = .182. For the related distracter condition, accuracy was higher for congruent trials than for incongruent trials, *t*(42) = 5.49, p < .001, while there was a similar trend for the unrelated distracter condition, *t*(42) = 1.85, p = .071; see Figure 6.2a). Thus, participants benefited more from congruent action-colour cues when the targets were presented among related rather than unrelated distracters.

For the *colour* task, the main effects of Distracter, F(1,42) = 290.82, $p < .001$, $\eta_p^2 = .874$ (related > unrelated), and Congruence, F(1,42) = 23.39, $p < .001$, $\eta_p^2 = .358$ (congruent > incongruent) reached significance. Finding matching framed coloured objects was more accurate when the search array contained semantically related objects. There was also a significant distracter by congruence interaction, F(1,42) = 110.08, $p < .001$, $\eta_p^2 = .724$. For the unrelated distracter condition, accuracy was higher for congruent trials than for incongruent trials, *t*(42) = 9.06, $p < .001$, while there was no reliable difference between congruent and incongruent trials in the related distracter condition (Figure 6.2b).

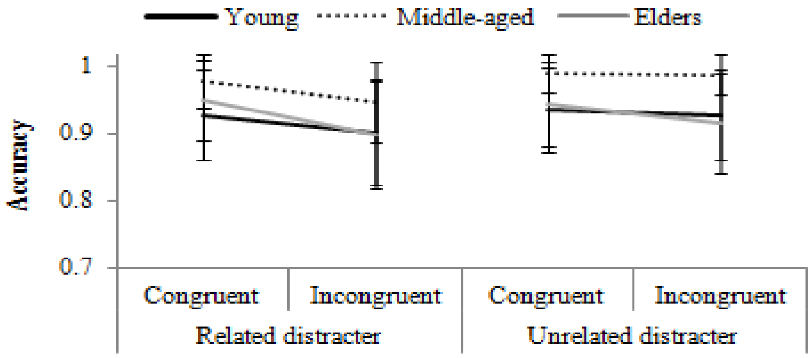
Age had a main effect on accuracy, F(2,40) = 4.03, p = .026, $\eta_p^2 = .168$. There was also a significant interaction between task and age, F(2,40) = 6.01, p = .005, $\eta_p^2 = .231$. This interaction showed that middle-aged participants were more accurate than both young and elderly participants in the action task but not in the colour task (middle-aged: *t*(13) = 6.41, $p < .001$, young and elderly: both $p > .099$). Young and elderly participants did not differ in their performances (see Figure 6.2a and Figure 6.2b). The distracter by age interaction was also reliable, F(2,42) = 3.85, p = .030, $\eta_p^2 = .161$. The two-way interaction arose because the overall benefit from semantically related distracters was enhanced with increased age, an effect that was mostly pronounced in the colour task (Figure 6.2c).

In light of the above three-way interaction observed across the age groups (i.e., Task x Distracter x Congruence), and to better understand how age modulated the overall pattern of results, we next computed 2 (Task) x 2 (Congruence) ANOVAs for each distracter condition and age group (Figure 6.2a and Figure 6.2b).

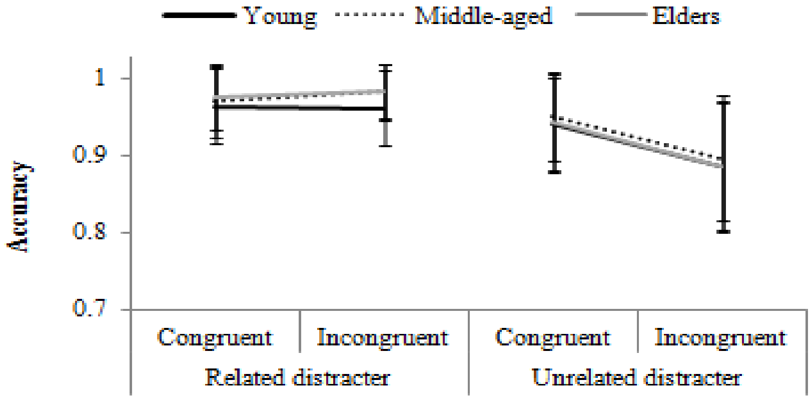
Related distracter condition: For young participants, there was only a reliable main effect of Task, F(1,14) = 17.34, p = .001, η_p^2 = .553 (colour > action). For middle-aged participants, the main effect of Task, F(1,13) = 9.87, p = .008, η_p^2 = .432 (colour > action), and the task by congruence interaction were significant, F(1,13) = 13.44, p = .003, η_p^2 = .508. This interaction arose because middle-aged participants' accuracy in the action task was higher for congruent compared to incongruent trials, *t*(13) = 4.81, p < .001, while there was no significant difference between congruent and incongruent trials in the colour task (p = .174). For elderly participants, reliable effects were observed for Task, F(1,13) = 16.22, p = .001, η_p^2 = .555 (colour > action), Congruence, F(1,13) = 12.81, p = .003, η_p^2 = .496 (congruent > incongruent), and for the interaction between task and congruence, F(1,13) = 10.96, p = .006, η_p^2 = .457. As with middle-aged participants, elders performed better in the action but not in the colour task when the trials were congruent compared to incongruent (*t*(13) = 4.31, p = .001, *t*(13) = -.65, p = .528, respectively). In summary, semantically related distracter and congruent action-colour cues had a similar impact on middle-aged and elderly participants compared to younger participants. In all three age groups, selecting functional pairs among semantically related distracters was more difficult than when participants had to select the same coloured-framed targets. For the young participants this effect was independent of cue congruence, while middle-aged and elderly participants showed this effect primarily during congruent trials (when the functional pair also had the same coloured frame). Taken together, these results suggest that in the context of semantically related distracters middle-aged and elderly participants relied more on integrating information from different cues modalities (action and colour) than young participants.

Unrelated distracter condition: For young participants, there was a reliable main effect of Congruence, F(1,14) = 16.49, p = .001, η_p^2 = .541 (congruent > incongruent), and an interaction between task and congruence, F(1,14) = 4.70, p = .048, $\eta_p^2 = .251$. Young participants were more accurate in the colour task but not in the action task when the trials were congruent relative to when they were incongruent, (*t*(14) = 5.06, p < .001, *t*(14) = .509, p = .619, respectively). For middle-aged participants, the main effects of Task, F(1,13) = 194.61, p < .001, $\eta_p^2 < .001$ (action > colour), Congruence, F(1,13) = 34.76, p < .001, $\eta_p^2 = .728$ (congruent > incongruent), and the interaction between task and congruence, F(1,13) = 14.63, p = .002, $\eta_p^2 = .529$, were significant. As the young participants, middle-aged participants' accuracy was higher in the colour but not in the action task for congruent relative to incongruent trials, (*t*(13) = 5.49, p < .001, *t*(13) = .193, p = .850, respectively). For elderly participants, there was only a significant main effect of Congruence, F(1,13) = 25.45, p < .001, $\eta_p^2 = .662$ (congruent > incongruent). To sum up, the young and middle-aged group showed a similar pattern which was different from the older participant group. Young and middle-aged participants benefited from the combined action-colour cue in the colour task but not in the action task, while elders benefited from the combined action-colour cue in both tasks to the same degree.

(a) Action task



(b) Color task



(c) Semantic relatedness

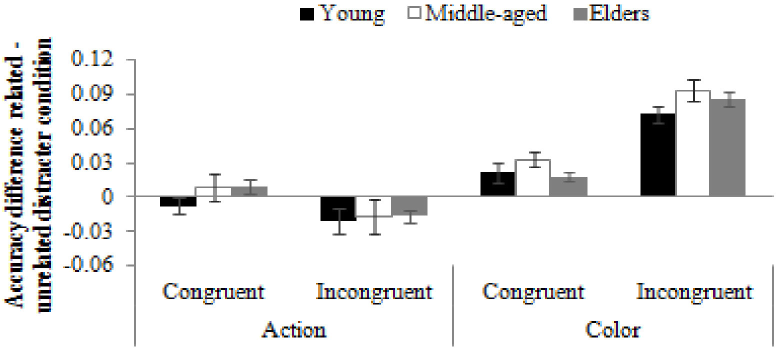


Figure 6.2. Mean accuracies for the interaction between distracter, congruence and age plotted separately for the (a) action task and the (b) colour task with standard errors of the mean (SEM). (c) Accuracy difference (with SEMs) between the related and the unrelated

distracter condition as function of task (action, colour) and colour congruence (congruent, incongruent).

zRTs. There were significant main effects of Task, $F(1,40) = 816.84$, $p < .001$, $\eta_p^2 = .953$ (colour > action), and Congruence, $F(1,40) = 35.35$, $p < .001$, $\eta_p^2 = .469$ (congruent > incongruent. There were reliable interactions between task and congruence, $F(1,40) = 11.64$, $p = .001$, $\eta_p^2 = .225$, and between distracter and congruence, $F(1,40) = 7.93$, $p = .008$, $\eta_p^2 = .165$. For both tasks, responses were faster for congruent trials than for incongruent trials (action task: $t(42) = -5.16$, $p < .001$; colour task: $t(42) = -2.39$, $p = .021$; see Figure 3a). For both distracter conditions, participants were faster in the congruent compared to the incongruent condition (related distracter: $t(42) = -3.15$, $p = .003$; unrelated distracter: $t(42) = -6.41$, $p < .001$; Figure 6.3b).

Similarly to the accuracy data, age had a reliable effect on response time to correct trials[1], $F(2,40) = 6.74$, $p = .003$, $\eta_p^2 = .252$; see Appendix 4). Bonferroni corrected multiple comparisons showed that middle-aged participants were significantly faster than older participants ($p = .003$) and marginally faster than young participants ($p = .051$), while there was no significant difference between young and older participants ($p = .763$). As before, there was a significant interaction between task and age, $F(2,40) = 4.37$, $p = .019$, $\eta_p^2 = .179$ (Figure 6.4). Across all participants, responses were slower in the action compared to the colour task, with the effect being strongest for the two younger participant groups (young: $t(14) = 19.22$; middle-aged: $t(13) = 17.72$; elders: $t(13) = 13.08$, all $p < .001$).

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[1] We note that the standardisation procedure of the RT data included all trials (correct + incorrect), while only correct trials were included in the zRT analysis. The latter one explains the possibility to observe differences between individual zRT averages.

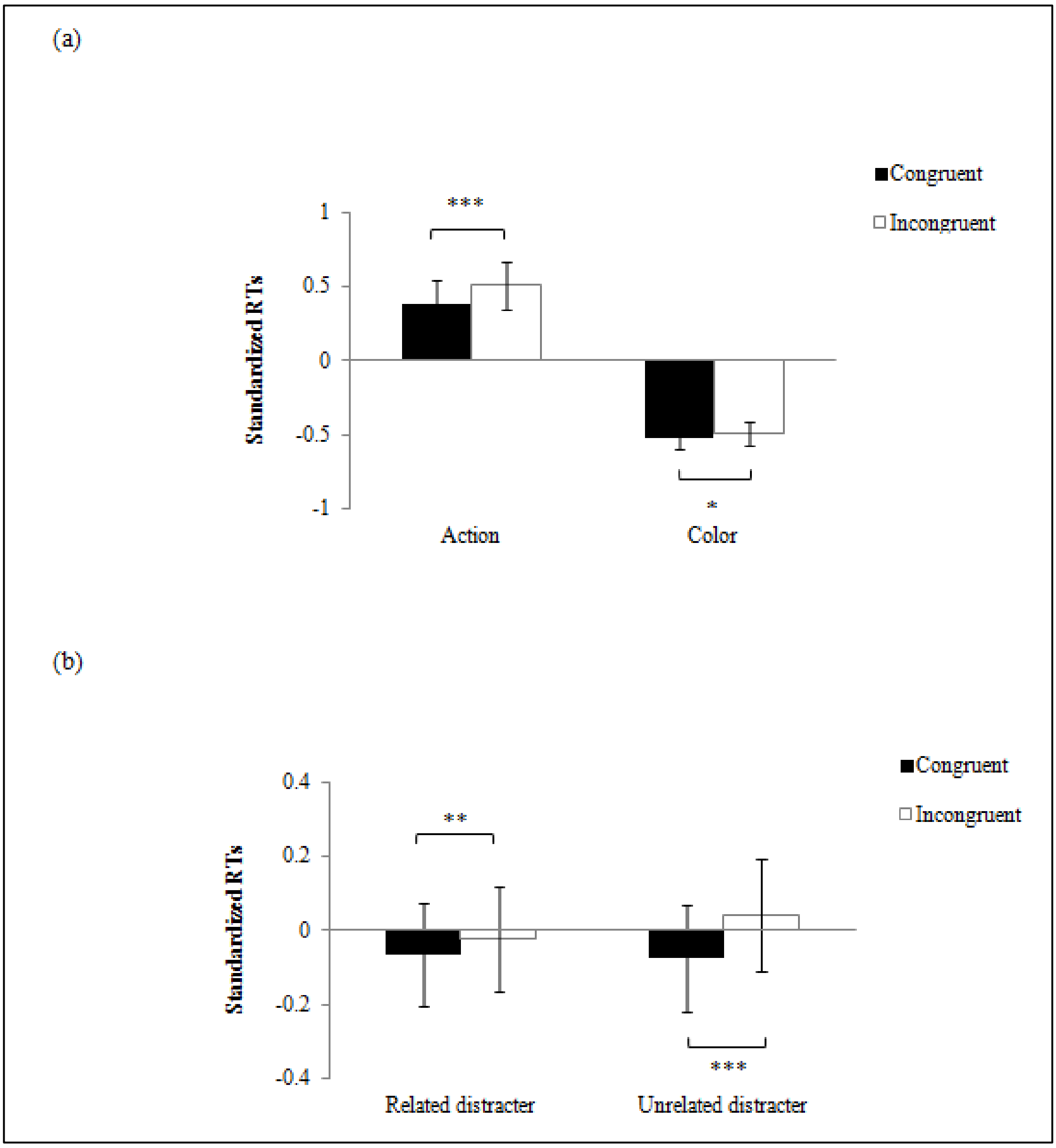

Figure 6.3. Mean zRTs (with SEMs) for the interaction between task and congruence (a) and between distracter and congruence (b). Asterisk denotes significance (***p < .001; **p < .01).

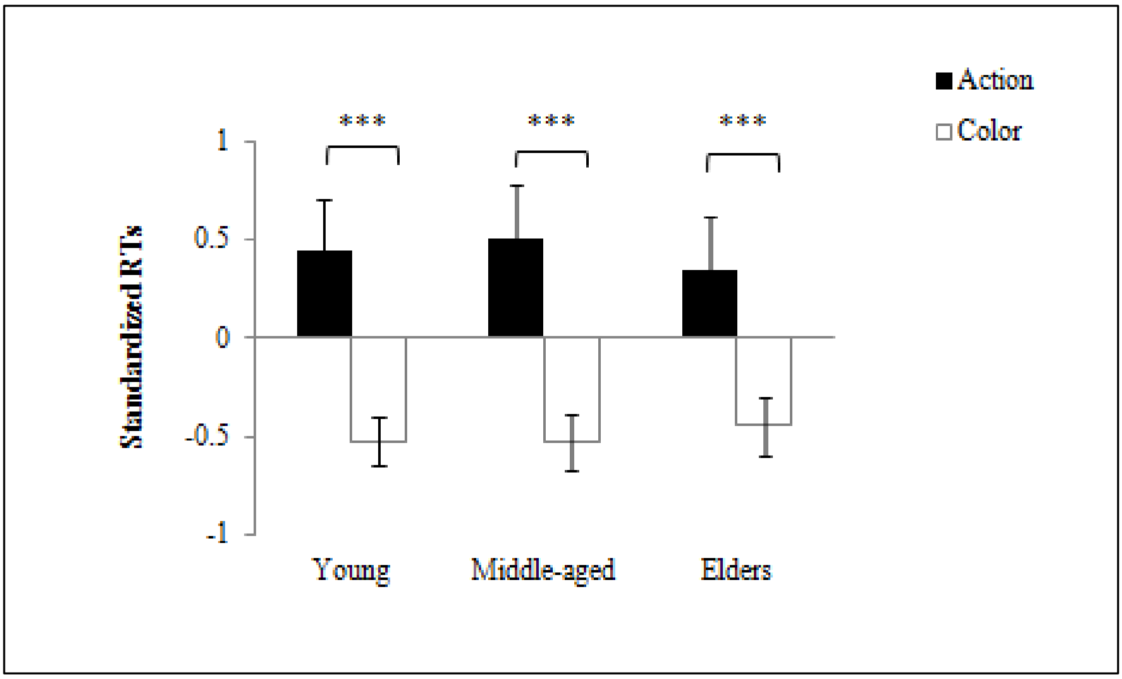

Figure 6.4. Mean zRTs (with SEMs) for the interaction between task and age. Asterisk denotes significance (***p < .001).

Contribution of procedural knowledge – selection of the active versus the passive object first. We first assessed whether across participants in each of the four conditions [2 (Task) x 2 (Distracter)] participants reliably selected the active object before the passive object (> 50% of trials) using one-sample *t*-tests and Bonferroni multiple comparisons correction. Then we tested the effects of the conditions on the contribution of procedural knowledge using a repeated-measures ANOVA with the following within-subject factors Task (action, colour), Distracter (related, unrelated), and Side of Active Object (left, right); Age (young, middle-aged, and older) was a between-subject factor.

For the action task, participants reliably selected the active object before the passive object in both the semantically related (mean active first = .66; *t*(39) = 10.81, p < .001) and semantically unrelated (mean active first = .65; *t*(39) = 8.42, p < .001) distracter condition. Across participants, the active object was not reliably selected before the passive object in the colour task.

The ANOVA revealed a significant main effect of Task, F(1,37) = 137.92, p < .001, η_p^2 = .788, indicating that participants chose the active object first significantly more often in the action than in the colour task. There was no main effect of age, nor was there an interaction with age. The task, distracter by side of active object interaction was reliable, F(1,37) = 5.20, p = .028, η_p^2 = .123 (see Figure 6.5). This interaction was decomposed by conducting separate 2 x 2 ANOVAs for each task.

For the *action* task, there was a reliable main effect of Side of Active Object, F(1,39) = 9.50, p = .004, η_p^2 = .196 (right > left) and a significant distracter by side of active object interaction, F(1,39) = 4. 26, p = .038, η_p^2 = .106. For both distracter conditions, the active object was selected first significantly more often on the right compared to the left side (related: *t*(40) = -2.53, p = .016; unrelated: *t*(40) = -3.39, p = .002).

For the *colour* task, only the main effect of Distracter, F(1,39) = 5.33, p = .026, η_p^2 = .120 (related > unrelated) was significant. Participants selected the active object first more often when the search array contained related than unrelated distracters.

To ensure that the effect of side of active object was not driven by the responding hand, we compared zRTs when participants selected the first object on the left and when they selected the first object on the right side. There was no significant difference between the left and the right side (p = .890), indicating that the effect of side of active object was independent of the response hand.

In summary, the active was selected in the action task more often first than the colour task. In the action task, this effect was more pronounced when the active object was on the right side. In the colour task, the active object was selected more often when the distracters were semantically related. Age did not reliably affect the selection order.

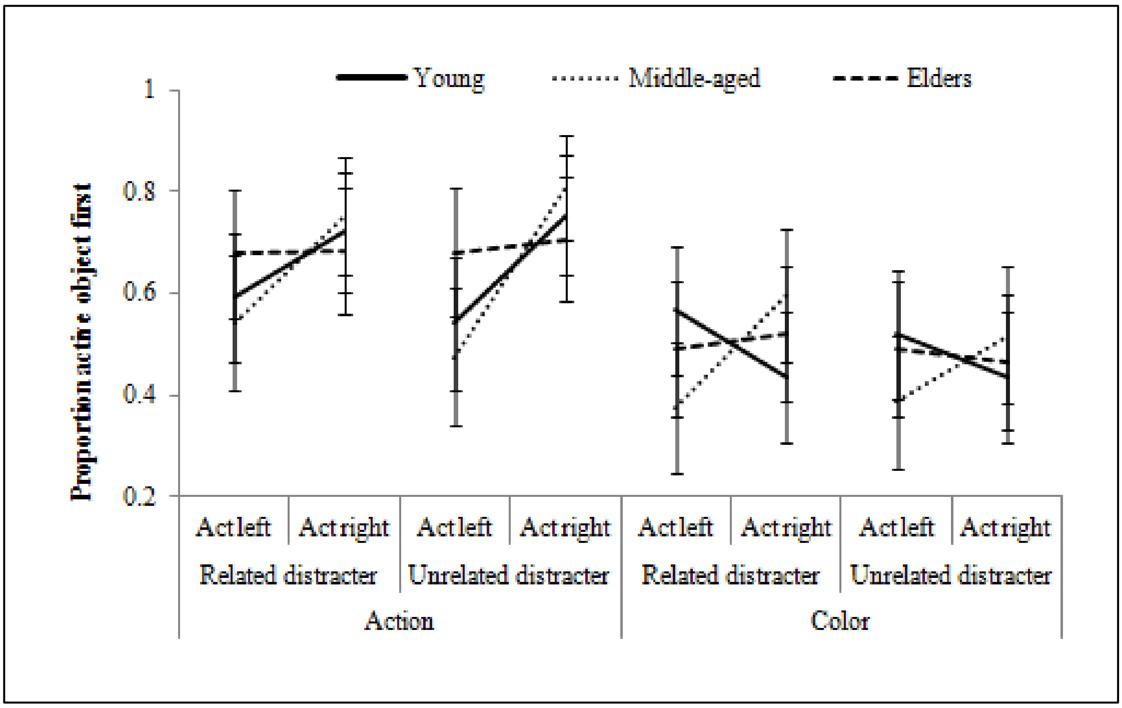

Figure 6.5. Mean proportion of selecting the active object first for congruent trials as function of task (action, colour), distracter condition (related, unrelated), side of active object (left, right) and age (with SEMs). Act = Active object.

6.5 Discussion

The present chapter revisited the questions regarding the contribution of semantic knowledge (indirect route) and procedural knowledge (direct route) to the retrieval of action knowledge manifested by paired-object affordances. More specifically, we investigated the relation between semantic and procedural knowledge during a conceptual-action (searching for an action pair) and a visual-colour (finding matching colour frames) search task. This enabled us to evaluate the explicit and implicit processing of functional object pairs, respectively. The contribution of the indirect-semantic route was assessed by manipulating the relation between targets and distracters, while the contribution of the direct-procedural route was tested by examining the order in which participants selected the targets. Finally, we also explored the effects of age across the lifespan on the ability to retrieve and utilise action knowledge.

The main findings are summarised as follows: (1) Semantic knowledge affected both types of searches but in an opposite direction. When distracters were semantically related to the targets, semantic knowledge interfered with the selection of objects for actions (action task) but facilitated the selection of objects that had the same coloured-frame (colour task). The contribution of semantic knowledge linearly increased with age. (2) Procedural knowledge reliably affected the way objects were selected but only when the task explicitly required the retrieval of action knowledge (action task). The contribution of procedural knowledge was not modulated by age. There was a tendency to utilise procedural knowledge even in the colour (implicit task) when the distracters were semantically related to the coloured targets. (3) Participants integrated action and colour cues in both tasks (congruence effects), with an age-related increase in cue integration. (4) There was an advantage for middle-aged participants compared to young and elderly participants in the action task, with young and elderly participants not showing a reliable difference. We discuss each of these effects separately.

6.5.1 Effects of procedural knowledge – selection priority for the active object – direct route for action retrieval

In the context of functional object pairs, one object is acting upon a second passive object, we replicated the bias toward the active object within an action pair in the action task (for neuropsychological evidence, see Wulff et al., 2015; Wulff & Humphreys, 2013; Riddoch et al., 2003; see also e.g., Laverick et al., 2015; McNair & Harris, 2014; Roberts & Humphreys, 2010b, for experimental evidence). The preference for selecting the active object (the tool) first is consistent with attention being biased toward the tool (e.g., Xu et al., 2015; Wulff & Humphreys, 2015, 2013; Handy et al., 2003). However, when action relations were irrelevant to the task (as in the colour search task) selection was not biased. This suggests that procedural knowledge is primarily used when making explicit action-related decisions but not when decisions are unrelated to actions. This result highlights the role of task demands/relevance on the retrieval of procedural knowledge. Interestingly, even in the colour-based selection task procedural knowledge had some impact on search performance as evident by a reliable performance difference when distracters were semantically related rather than unrelated to the targets (Figure 6.2). It could be that the increase in performance in the related distracter condition was partly related to the use of action cues. It is possible that when action pairs are presented in their “natural” context, the likelihood to “automatically” utilise procedural knowledge is higher. We propose that the bias toward the active object is weakened when is task is not action-relevant (visual-based selection in the colour task), whereas the bias toward the active object is increased when the task is action-relevant (action pair selection in the action task).

An alternative account for the above results is that the results may be driven by the conventional structure of language. In everyday language the order of objects is important, with active sentences (a hammer is driving in nails) being more common than passive sentences (a nail is driven in by a hammer). The relation between complex actions and language processing is a matter of intensive debate (e.g., Glenberg & Kaschak, 2002) as well as how much language is developed based on our embodied cognition and knowledge of actions (Pulvermueller & Fadiga, 2010). Converging evidence has shown a strong relationship between language and action, assuming that language comprehension is grounded in bodily actions by simulating or reactivating motor experience (e.g., Glenberg & Kaschak, 2002; Barsalou, 1999). Thus, it is unclear whether the similarity between procedural knowledge and the structure of language is incidental or whether procedural knowledge underlies the structure of active sentences.

It could also be that selection priority for the active object is not because selection is guided by procedural knowledge but due to other strategies. For example, to complete the action task participants have to keep the identity of one object in working memory while looking at other objects as functional partner candidates. After identifying a potential functional object pair, participants may want to verify that the potential pair actually functions together, especially in the presence of distracters. Hence the selection priority arises from the verification process rather than the initial selection.

In the action task, the observed selection priority for the active object was sensitive to the location of the active object – the active object was prioritised more when it appeared on the right rather than on the left side. This effect was pronounced in the unrelated distracter condition. The effect of presentation side of the active object matches previous studies with healthy participants and neuropsychological patients, showing a performance benefit when the spatial arrangement of the active and passive object matched the participant's preferred handedness (Yoon et al., 2010; Humphreys et al., 2010a). This raises the question whether this effect was also driven by the syntactic structure of sentences. Yoon et al. (2010) asked participants to make action and semantic decisions to pairs of objects (written words), with the active object on the left and the passive object on the right and vice versa. For action decisions, responses tended to be faster when the active object was on the left side compared to when it was on the right side (e.g., pen-paper vs. paper-pen; respectively), whereas there was no difference in response times when making semantic decisions. The authors suggested that this pattern might reflect the spatial order of written English sentences where the active object precedes the passive object, and hence appears to the left of the passive object. However, if the preference for the active object first reflects linguistic constructions, then we would expect that participants would select the active object more often on the left side rather than on the right side. It was not the case in the present study – participants selected the active object on the right (vs. left) side more often in the action task, while there was no location priority in the colour task. It is also possible that participants simply selected first the object that was closer to their responding hand. If this was the case we would expect a similar presentation side advantage in the colour task which we did not observe. Moreover, we did not find a reliable difference in response time between selecting the first object on the left compared to the right side. Interestingly, in the colour task, the active object was prioritised only in the related distracter condition independent of its position in the search array. This result seems to be in line with the performance of extinction patients (Wulff & Humphreys, 2013; Riddoch et al., 2003) who also prioritised the active object over the passive object independent of its location in space when reporting the name of the object.

The retrieval of procedural knowledge has been associated with the dorsal visual stream, specifically the ventro-dorsal substream (Binkofski & Buxbaum, 2013; Buxbaum & Kalenine, 2010; Rizzolatti & Matelli, 2003). Mounting evidence has indicated that the dorsal route is sensitive to whether or not the object is aligned with the participants' preferred hand (e.g., the teapot is held by the right (dominant) hand). For example, hand alignment effects have been reported in pre-motor, motor, and parietal cortices (e.g., Drew et al., 2015; Proverbio et al., 2013; Buccino et al., 2009). Moreover, a recent lesion subtraction study revealed that lesions to pre-motor, parietal and temporal cortices were associated with reduced effects of hand grip on action decisions and with a diminished priority for the active object (Wulff et al., 2015).

The involvement of fronto-parietal regions in the retrieval of action knowledge has been also reported in a comprehensive review by Noppeney (2008). Thus, we speculate that the effects of hand alignment and the bias toward the active object were mediated by fronto-parietal regions, although it obviously requires further investigation.

We did not find conclusive evidence that action cues were used in the colour task. Although we observed cue congruence effects in the colour task, this effect was driven by unrelated but not by related distracters. In the unrelated congruent distracter condition, the targets differed from the distracters based on their functional relation and their semantic category. In contrast, in the related congruent distracter condition, the targets differed from the distracters only in their functional relation. In the latter case, there was no evidence for action-colour cue congruence. Thus, the data suggest that semantic relatedness had implicit effects on colour decisions but not on functional knowledge.

Taken together, the present results suggest that procedural knowledge is not automatically retrieved. The degree to which procedural knowledge was used to guide selection processes depended upon task relevance and the context in which objects were presented. In the action task, participants utilised procedural knowledge to select functional object pairs, favouring the active object that is positioned for a right hand action (cf. Laverick et al., 2015). The results are in line with the direct route for action retrieval (Riddoch et al., 1989).

6.5.2 Effects of semantic distracters – indirect semantic route for action retrieval

The present chapter showed that semantic processing affected retrieval of action knowledge. The involvement of the indirect semantic route was tested by manipulating the relation between targets and distracters. We demonstrated that the relevance of the task (i.e., action-relevant or not) influenced the recruitment of the semantic route. The presence of semantically related distracters disrupted performance in the action task, while it improved performance in the colour task. In both tasks the impact of semantic processing on target selection was enhanced for incongruent trials (coloured targets which did not form an action pair). The distracter effect in the action task is in accord with previous studies, showing that semantically related distracters interfere with action decisions (Wulff et al., 2015; Laverick et al., 2015). This is an intriguing finding as one would expect that action decisions would be facilitated in the context of a familiar environment (e.g., finding a knife and a fork among other items in the kitchen). This may suggest that objects are not represented based on their functional relation but primarily based on their categorical features (e.g., used in the kitchen). In this case, all objects from the same category have the potential to interact, and thus action decisions are hampered due to the non-specific potential for action as stored within the semantic route.

The question arises as to why semantic relation had such a large effect in the colour task. We speculate that effects of semantic relation in the colour task may be due to the fact that colour processing occurs in the ventral visual stream (Zeki, 1990), which is part of the indirect route. Nevertheless, further research is needed to clarify the association between colour-based selection and semantic processing. It is important to note that the effects of semantic relation in the colour task were primarily driven by semantically unrelated incongruent trials. In these trials the coloured targets were from different semantic categories, and one target was functionally and semantically associated with one of the distracters. This could have made the selection process more difficult compared to semantically related congruent trials where colour targets were always functionally related (Figure 2c).

The ventral (anterior temporal) visual pathway is activated during semantic processing (for recent reviews, see Visser, Jefferies, & Ralph, 2010; Noppeney, 2008; see also, Goodale & Milner, 1992). We assume that anterior temporal regions were involved in processing the semantic relations between targets and distracter.

In summary, the present results support the involvement of semantic knowledge during explicit (finding functionally related objects) and implicit (colour frame matching) action retrieval demands. The data are consistent with the indirect semantic route from vision to action (Riddoch et al., 1989).

6.5.3 Retrieval of action knowledge across the lifespan

We first demonstrated that retrieval of action knowledge changes across the lifespan. Firstly, middle-aged participants performed better than young and older participants in the action task. The results show an inverted U-shaped performance pattern across the lifespan increased performance in middle-aged adults which then decreases in late life (cf. Potter et al., 2012; Waszak et al., 2009). This is in line with the assumption that cognitive development across the lifespan follows an inverted U-shaped function (e.g., Dempster, 1992). Could this be explained by a general cognitive advantage of middle-aged adults, who also happen to be more educated? We think this is unlikely, since the advantage of the middle-aged group was specific to the action task and was not observed in the colour task. We propose that the midlife performance advantage in action retrieval reflects the impact of life experience in using and operating objects (cf. performance advantage for middle-aged participants in terms of divergent thinking; Reese et al., 2001). Our young participants were university students who by and large experienced less than two years of independent living. Hence their experience in using specific kitchen and garage items was relatively limited (even though they are visual familiar with these objects). In this context it is difficult to account for the decline observed in elders, though it may be related to other sensory (e.g., identifying the pictures) or motoric factors specific to the task. Further research is needed to clarify this point. This finding, however, stresses the importance of investigating how cognitive processing changes across the entire lifespan rather than focusing only on early and/or late adulthood as changes across the lifespan are not always linear.

A second finding was that effects of semantic relation between target and distracters increased with age. This effect was primarily observed in the colour task (Figure 2c), and thus it is of less relevance to the main questions of the present study. Detailed analyses were carried out to disentangle the impact of distracter type on age as function of task and congruence. The data showed linear changes across the lifespan in the way action and colour cues were used. In the related distracter condition, there was evidence for an integration of action and colour cues in middle-aged and elderly but not young participants. In the action task, integrating action and colour cues improved performance, while it had no effect on performance in the colour task. In the unrelated distracter condition, young and middle-aged participants benefited from the combined action-colour cues in the colour task, while elders benefited from it in both tasks. Recall that action cues in the unrelated condition are inherently confounded by the semantic relatedness of targets and distracters. Nevertheless, the data showed that across the lifespan the integration of different cue types (e.g., action and colour) increases. This is line with previous studies (e.g., Yankouskaya, Rotshtein, & Humphreys, 2014; Laurienti, Burdette, Maldjian, & Wallace, 2006). It seems that with increasing age it was more difficult to ignore task-irrelevant information as evident by the integration of action and colour cues.

To sum up, the present study shows some effects of age on the retrieval of action knowledge. While the direct route was not affected by age (i.e., age did not modulate the selection order the objects), the semantic route was modulated by age (effects of distracters increased with age). Furthermore, there was evidence for an integration of different cue information with increasing age. Based on these results, it can be speculated that there is a different weighting of the two routes with age, with a primacy of the direct route as highlighted by the midlife advantage. However, the extent to which age modulates the involvement (weighting) of the two routes requires further investigations.

6.6 Study limitations

We acknowledge that the present elderly sample included mostly men, the young participants were all female, while the middle-aged group was equally matched for gender. It is therefore difficult to know how gender contributed to the observed age effects. However, we note that the effect of age, the inverted U-shaped performance in the action task, cannot be explained by gender differences. In addition, previous literature has demonstrated that there are no gender differences (e.g., Borghi et al., 2012). The effects of age could also be potentially confounded by the level of education. In the present study, young participants (i.e., undergraduate students) spent fewer years in education than the middle-aged participants, while middle-aged participants spent more time in education than most of the elderly participants. Thus, years in education could contribute to the results in multiple ways (e.g., familiarity with the computer interface, motivation, intelligence, executive functions). However, if this would be the case, we would expect that education affects overall performances rather than being specific to the task or condition, as reported here. The observed effect of semantic distracter in the implicit search task could be due to the nature of the targets on incongruent trials. In contrast to the congruent condition, the coloured targets were from different semantic categories and thus could have confounded the results. This potential limitation certainly deserves more attention in future studies.

6.7 Conclusion

The presence of paired objects affected search performance explicitly with some evidence for implicit effects with increased age. This highlights the role of task relevance on selection processes. The results confirm effects of procedural knowledge associated with paired objects in the context of an action (explicit) search task, supporting the direct (probably via the ventro-dorsal substream) route from vision to action. The presence of semantically related distracters affected performance differently in both tasks, indicating that action and non-action-related features are processed in the indirect semantic (ventral) route from vision to action. Finally, effects of action knowledge were modulated by age.

CHAPTER 7: GENERAL DISCUSSION AND CONCLUSIONS

The present thesis systematically investigated the effects of paired-object affordance on attention and perception in different contexts. Paired-object affordance effects arise when there is improved responding to object pairs that are positioned for action compared with object pairs not so positioned. The effect is assumed to be due to both a visual-related response to the visual familiarity of the object pair (varying as a function of object orientation and perspective) and a motor response to possible actions evoked by the objects (manipulated by hand grip/hand alignment; Humphreys et al., 2013; Humphreys et al., 2010a). The present thesis examined the neural basis of the paired-object affordance effect and the impact of contextual information and task demands on the perception of paired-object affordance. In a series of five experimental studies, the thesis aimed to shed light on these topics.

The findings of these studies will first be summarised (see Table 7.1), then followed by a synthesis of the present results linked to existing theoretical frameworks and subsequently future research will be briefly discussed. Finally, an overall conclusion of the thesis will be drawn.

7.1 Summary of thesis

Table 7.1 Summary of all the results of the present thesis

Component		Effect	Healthy participants	Extinction patients
Visual-based affordance	Action relation	AR > NAR	✓Ch2,3	✓Ch4,5
	Perspective	1PP > 3PP	✓Ch2	
		3PP > 1PP		✓Ch4
	Familiarity	Fam > Unfam		✓Ch5
Motor-based affordance	Hand alignment	RH > LH	✓Ch6	
		LH > RH	✓Ch2,3	✓Ch4,5
	Graspability	Broken tool > Intact tool		✓Ch5
		Active > Passive	✓Ch6	✓Ch4,5*

Note. AR = action relation; NAR = no action relation; 1PP = first-person perspective; 3PP = third-person perspective; RH = right-handed action; LH = left-handed action; Fam = Familiar object pair; Unfam = unfamiliar object pair; Ch = chapter.

*Based on extinction trials.

The first two experimental chapters investigated the neural mechanisms underlying paired-object affordance in healthy participants. Chapter 2 revealed that visually-based affordance cues (varied by manipulating the orientation and position of objects) activated the IPL bilaterally, with increased responses to objects correctly positioned for action compared to objects incorrectly positioned for action. Motor-based affordance cues (manipulated by varying the alignment of a hand with the object) activated the SMA and the cerebellum, with enhanced responses to non-dominant hand assignments (cf. Chapter 3; Kelly et al., 2015; but behaviourally the opposite result has been reported, Yoon et al., 2010; Humphreys et al., 2010a). In these regions, activation was increased for object pairs viewed from a 1PP. The novel result was that paired-object affordance effects seem to be mediated by interactions between different networks processing visual- and motor-based affordance cues, respectively (cf. Humphreys et al., 2013; Humphreys et al., 2010b).

In Chapter 3, the role of M1 in paired-object affordance was further studied using TMS-induced MEPs. The results showed that only the right (non-dominant) M1 was sensitive to the experimental manipulations. Excitability of the right M1 was enhanced when two objects were positioned to afford an action, with stronger responses when the tool was gripped by the non-dominant hand compared to when it was gripped with the dominant hand (cf. Chapter 2). The observed motor response seems to reflect the alignment with the tool as motor excitability for non-action-oriented objects also tended to be enhanced when the tool was presented in non-standard (left) hand positions. As previously discussed in Chapters 2 and 3, increased responses to non-dominant hand alignments may reflect unfamiliarity with the observed action (e.g., Hoeren et al., 2013; Liew et al., 2013; Cross et al., 2012). Interestingly, an effect of hand posture was only observed when the objects were not positioned for action, with greater MEPs when the perceived potential for action was high (in case of neural hand postures). The data suggest that M1 excitability is modulated by cognitive processes supporting paired-objects affordance, in particular processes involved in evaluating the action potential of the active object within object pairs.

Chapters 4 and 5 were both concerned with the effects of paired-object affordance on visual extinction by manipulating visual-based affordance cues (manipulating familiarity with the object pair; Chapter 4) and motor-based affordance cues (manipulating graspability of the stimuli; Chapter 5). For these two chapters, I measured object identification performance (i.e., in particular whether there was recovery from extinction) as an index of attentional allocation. Chapter 4 showed that unfamiliar but action-oriented object pairs ameliorated extinction, replicating the findings previously observed with familiar action-oriented objects (Humphreys et al., 2010a; see also, Riddoch et al., 2006; Riddoch et al., 2003). Chapter 5 further supported this argument that familiarity with the action pair is not crucial for the affordance effect. Here recovery from extinction was higher for both action-related object pairs and unrelated tool pairs compared to unrelated object pairs (note that there was no significant difference in extinction recovery rate between the former two pairs). This suggests that the potential for action rather than the motor/visual familiarity with the object pair is responsible for the perception of affordance (cf. Riddoch et al., 2006). Furthermore, the results revealed that the presence of a tool regardless of its relation to the other object is important for the affordance effect. Interestingly, in both studies recovery from extinction was increased when the tool appeared on the contralesional (i.e., the non-dominant hand position) than on the ipsilesional side (cf. Chapter 2 and 3). Moreover, the analysis of extinction trials, when only one of two items was correctly reported, showed a bias towards the tool, even if the tool fell on the contralesional side (cf. Riddoch et al., 2003). As discussed in Chapters 4 and 5, the error data suggest that attention was biased to the tool rather than the passive object. Specifically, attentional capture by the ipsilateral item disrupted report of the contralesional item (increased extinction), while the opposite pattern occurred when attention was cued to contralesional item (less extinction).

In Chapter 5, the impact of a broken handle on the perception of paired-object affordance was assessed. When the tool was intact, patients reported more action-related objects when the tool appeared on the contralesional (vs. the ipsilesional) side. This did not occur when the handle of the tool was broken. The data suggest that breaking the handle of a tool but not an object lessens the degree to which the tool captures attention, with attentional capture being strongest when an intact tool appears on the ipsilesional side (cf. Chapter 4). Overall, the results of both studies suggest that the perception of paired-object affordance is influenced by both visual-based affordance cues (familiarity with the object pairs, the perspective, and action relation) and motor-based affordance cues (graspability and hand alignment).

The last experimental chapter directly explored the role of contextual information and task demands on the automatic perception of paired-object affordance effects across the lifespan. When participants searched for action pairs (a task requiring an explicit response to action-related stimuli) the tool was selected before the passive object in a pair, replicating the attentional bias towards the tool previously observed in healthy participants and patients (cf. Chapter 4 and 5; see also, e.g., Wulff et al., 2015; Xu et al., 2015; Riddoch et al., 2003; Handy et al., 2003). In line with prior research (e.g., Yoon et al., 2010), the tool was prioritised when it appeared on the right side (the standard hand position). However, the opposite result was found in Chapters 4 and 5. The inconsistency of the findings is likely due to task instructions. Participants in the study by Yoon et al. (2010) and Chapter 6 were explicitly instructed to use action knowledge (making action decisions), while a naming task was used with extinction patients (Chapter 4 and 5; Humphreys et al., 2010a); this latter task did not require to retrieve action knowledge. Chapter 6 also revealed effects of age on the retrieval of action knowledge. Specifically in the action task, there was a performance advantage for middle-aged participants which decreased during late adulthood. When the task demands on action retrieval were implicit (participants searched for colour targets), the results of action affordance were weakened; for example, the tool was only selected first when the distracters were related, and there was no effect of tool location. This indicates that task instructions modulate the use of action affordance, with effects being pronounced when the task requires action-related decisions.

The presence of semantic distracters had an opposite impact on both tasks: performance was disrupted in the action task (cf. Wulff et al., 2015) but not in the colour task. The effect of semantic knowledge in the colour task could be confounded by the nature of the stimuli on incongruent trials (here one of the colour targets was functionally and semantically related with one of the distracters), and thus the data should be interpreted with caution (see future study suggestions, section 7.3). Overall, the results suggest that that the presence of paired objects affects search performance, but primarily when the task is action-related.

7.2 Paired-object affordance

Each of the five experimental studies of the thesis focused on different aspects of paired-object affordance effects. The results of all the studies highlight that paired-object affordance is influenced by contextual information and task demands, with the active object (the tool) within a pair modulating attentional allocation. In the following subsections, the results of the thesis will be integrated into existing theoretical frameworks.

7.2.1 Automaticity and the role of context and task demands

The automatic perception of affordance when viewing graspable objects is hotly debated (see, Borghi & Riggio, 2015; van Elk et al., 2014; Thill et al., 2013, for reviews). The results of the studies of this thesis support both the automatic perception of affordance (especially evident in Chapter 4 and 5) and the modulation of affordance perception by task (Chapter 6) and context (all chapters). Chapters 4 and 5 revealed that identification responses in extinction patients were implicitly influenced by the presence of action-oriented but not necessarily familiar object pairs (cf. Riddoch et al., 2006). Moreover, there was evidence for a preattentive processing of paired objects. On extinction trials, patients typically reported the tool rather than the passive object, regardless of the side of presentation (cf. Riddoch et al., 2003). Even though the action relation between the objects was task-irrelevant, patients' performance was implicitly influenced by the presence of action-related objects. This is in agreement with the direct (automatic) perception of affordance (cf. Gibson, 1979).

Previous research has used implicit measures when assessing the automaticity of affordance effects using non-ecological settings, typically stimulus-response compatibility paradigms (e.g., Xu et al., 2015; Tucker & Ellis, 1998). However, in everyday life we are surrounded by multiple objects and the affordances of these objects is influenced by the presence of other objects which can be semantically, functionally and/or spatially related (e.g., a kitchen contains cups, spoons, and plates placed left or right to each other). Using a more ecological approach (searching for targets among distracters), the results of Chapter 6 suggest that only explicit but not implicit task instructions (action pair vs. colour pair search, respectively) led automatically to the perception of action pairs. To the best of the author's knowledge, this is the first behavioural study which directly compared the influence of task demands on paired affordance perception. The influence of task instructions has been previously reported using neuroimaging (e.g., see meta-analysis by Caspers et al., 2010). For example, activity in the posterior parietal cortex, assumed to extract affordance (Jeannerod et al., 1995), was only evident when participants had to explicitly retrieve action knowledge compared with when they passively viewed objects. Thus, explicit task instructions facilitate the retrieval of action knowledge.

Across all chapters, the influence of contextual information on affordance was demonstrated. Presenting object pairs in a way that affords a mutual action facilitates performance in normal participants varying age and in patients (e.g., Wulff et al., 2015; Laverick et al., 2015; Xu et al., 2015; Bach et al., 2005). Familiarity with the object pair does not seem crucial for the occurrence of the affordance effect (Chapters 4 and 5). However, the presence of a tool within action-oriented pairs seems to be important for the perceived action potential (affordance), even if the pair is unfamiliar to the participants (cf. Riddoch et al., 2006). In addition, Chapter 6 revealed that the presence of distracters interfered with task performance in the explicit action task. Semantically related distracters disrupted search performance when selecting objects for action, indicating that selecting objects for action is influenced by the presence of semantic information (cf. Wulff et al., 2015; Laverick et al., 2015). Moreover, the result also implies that the selection of objects in a more realistic scenario relies on both the automatic extraction of affordance (including retrieving of procedural knowledge) and semantic processing (cf. dual-route model from vision to action; Riddoch et al., 1989).

To sum up, the present thesis advances knowledge about the automaticity of affordance and separates out factors that do and do not affect the automatic perception of affordance.

7.2.2 The role of attention in paired-object affordance

There is a lack of consensus about whether or not attention can modulate the occurrence of the affordance effect (for recent reviews, see Borghi & Riggio, 2015; van Elk et al., 2014; Thill et al., 2013). The results of the present thesis provide a first step towards a better understanding of the role of attention in affordance activation by presenting pictures of real-world objects in natural scenes (as opposed to single object presentations). In particular, the present results stress the role of tools in visual scenes (cf. Matheson et al., 2014; Handy et al., 2003). Chapters 4 and 5 directly provide evidence that affordance activation is associated with attentional allocation (cf. Riddoch et al., 2003). Objects that were co-located for action captured attention and were reported to a greater extent by extinction patients than objects that were not oriented for action. Preattentive grouping based on the affordance for action offered by interrelated objects was supported by trials where extinction occurred (cf. Riddoch et al., 2003). On those trials, there was enhanced report of the tool rather than the passive object irrespective of its location in the visual field, but only when the objects were oriented for action (Chapter 4; cf. Riddoch et al., 2003). Chapter 5 further demonstrated attentional capture from the tool within action-oriented object pairs, by showing that the attentional bias towards tools was diminished when the tool handle was broken but not when it was intact. This suggests that the action-related but task-irrelevant features of the tool automatically capture visual attention, and subsequent to this a visual response is elicited which influences attentional selection and the corresponding motor response (for neurophysiological evidence, see Matheson et al., 2014; Kumar et al., 2012; Buccino et al., 2009; for a review, see Humphreys et al., 2013). Converging evidence for attentional capture by the tool within an action-object pairing comes indirectly from the reported studies of this thesis with healthy participants, with performance being influenced by the location of the tool with respect to the hands the participants would normally use to perform the action.

Taken together, the thesis further supports the role of attention in the occurrence of the affordance effect (attention being captured by affordance) and also highlights the automaticity of affordance which guides visual attention.

7.2.3 Mechanisms underlying paired-object affordance

The results of the present thesis provide empirical evidence for the two suggested components of paired-object affordance (for recent reviews, see Humphreys et al., 2013; Humphreys et al., 2010b). Humphreys et al. assumed that paired-object affordance stems from a visual- and a motor-based response. Chapter 2 showed that paired-object affordance is mediated by different but interacting bilateral parieto-frontal networks. In line with the behavioural study by Humphreys et al. (2010a), it was found that viewing objects correctly co-located for action presented from a 1PP enhanced visual-based affordance responses in fronto-parietal regions. Motor responses to non-dominant hand actions were evident in SMA, with enhanced responses when non-dominant hand actions were seen from the 1PP. The different neural responses to visual- and motor-based affordance cues offered by paired objects imply that the effects of action relation and hand alignment were processed separately, and that the perspective manipulation (1PP) enhanced both effects. Using MEPs (Chapter 3), the effects of action relation and hand alignment on motor cortex were replicated. Specifically, greater MEPs were found for interacting objects misaligned with the hands the participant would normally use to act on the objects. As suggested in the discussions of Chapters 2 and 3, the increased motor cortex activity for non-dominant hand actions may reflect the degree of visual and/or motor familiarity with the observed action (cf. Calvo-Merino et al., 2006).

Further behavioural evidence for visual and motor responses to paired objects comes from the three behavioural chapters of the thesis. Chapter 4 revealed that familiarity with the object pair modulated motor but not visual response, with better performance to non-dominant hand actions (but see, Humphreys et al., 2010a). Chapter 5 provided further evidence that the visual response to object pairs is not affected by action familiarity. There was no advantage for action-related (object-tool) pairs compared to unrelated tool-tool pairs, although the rate of recovery from extinction for both pairings was higher than for unrelated object-object pairs. This indicates a general advantage for reporting tools over objects, and that possible actions have a higher weight than the familiarity with the pair. Thus, it seems that paired-object affordance effects do not entirely rely on learned functional relations between objects (for a different interpretation, see Humphreys & Riddoch, 2007). The perceived potential for action can determine whether extinction patients can detect the contralesional item, even if the contralesional item is an object. One other novel result in Chapter 5 was that the attentional bias towards the tool rather than to the passive object within a pair, as indexed through the recovery rate, was itself affected by the graspability of the tool – detection of the contralesional item was reduced when an intact tool appeared on the ipsilesional side (for reduced M1 excitability in healthy participants, see Buccino et al., 2009). This result again provides evidence for a motor response to paired objects.

Using a more complex stimulus display in Chapter 6, visual- and motor-based responses to paired objects were also evident, but only when the search task was related to action affordances. When searching for functional object pairs, performance was reduced when objects were surrounded by semantically related distracters. The semantic similarity between targets and distracters (e.g., all item were kitchen items but they are normally not used together) may have evoked multiple affordances, and thus affecting the allocation of attention and subsequent search performance. Learned associations between objects might be important for disambiguating competing affordances if the search display is complex (but see Chapters 4 and 5; cf. Humphreys & Riddoch, 2007). However, further research is needed to explore this possibility. Even though it was task-irrelevant, participants selected the tool before the passive object when selecting objects for action, with enhanced selection priority for tools when its location matched the participants preferred hands when performing actions (e.g., Xu et al., 2015; Yoon et al., 2010; Humphreys et al., 2010a).

Taken together, the present results indicate that visual and motor responses to paired objects are independent of each other, but interactions between these responses can occur which in turn enhances visual presentation of the observed objects, and thus attention (Humphreys et al., 2013; Humphreys et al., 2010a). The effects of paired-object affordance are assumed to be generated by enhanced responses in bilateral frontal motor-related and parietal visual-related regions.

7.2.4 Affordance in relation to other perception-action theories

The results of the thesis are in line with the dual-route model from vision to action (Riddoch et al., 1989). Evidence for the direct (non-semantic) route comes from the observed effects of hand alignment when viewing correctly co-located objects for action (cf. Yoon et al., 2010; Humphreys et al., 2010a). Viewing interacting objects in plausible locations for action (even when the tool was grasped with the non-dominant hand) automatically activates corresponding action representations bypassing semantic knowledge. This indicates that we are sensitive to perceived action affordances regardless of whether objects were in familiar or in unfamiliar locations for actions. Interestingly, the involvement of the direct route depends upon task demands. Chapter 6 showed that the direct route for action is only activated when the task is action-related (searching for action pairs) but not when the task is non-action related (colour search). In other words, attention needs to be directed to the objects in order to perceive their potential for action (see also, Tipper et al., 2006). Using a more realistic (complex) visual scene, Chapter 6 provided evidence for the recruitment of the indirect (semantic) route when selecting objects for action; search performance was disrupted when semantically related distracters were present (cf. Wulff et al., 2015; Laverick et al., 2015). Thus, if the environment is more ambiguous (in the presence of distracters), selecting objects for action requires the involvement of both the direct and the indirect semantic route from vision to action (e.g., Wulff et al., 2015; Laverick et al., 2015; Mizelle et al., 2013; Frey, 2007; Hodges et al., 2000).

As highlighted in the General Introduction, affordance effects are also related to other perception-action neurocognitive modules such as the tool network, the AON, and the MNS. Accumulating evidence suggests that activity in dorsal (PMC and IPL) regions of the tool network may reflect the neural substrate for affordance effects (e.g., Orban & Caruana, 2014; Osiurak et al., 2010; Rizzolatti & Matelli, 2003; Grezes & Decety, 2002). The present IPL activity when seeing interacting objects compared to non-interacting objects further confirms the automatic perception of affordance. IPL is assumed to store hand and finger movements in order to interact with objects (for a recent review, see Vingerhoets, 2014). However, note that the tool network is primarily concerned with tool affordance and tool use but not with the understanding of these observed actions.

It can be argued that understanding the action of another person is the focus of the AON (Grafton, 2009) and the MNS (Rizzolatti et al., 2001). Similarities and differences between paired-object affordance, the AON, and the MNS have been highlighted in Chapter 2. Even though the tasks of the present thesis did not explicitly require processing of the goal or the intention of the observed actions, implicit processing might have occurred. It is likely that an action goal was probably easier to perceive when objects were correctly positioned for action ("goal-directed actions") compared to when they were incorrectly positioned for action ("non-goal-directed actions"). Thus, brain regions associated with goal understanding could have been also automatically activated when viewing static pictures of pairs of objects as in Chapter 2. In line with this assumption are the results of Chapter 2 – viewing action-oriented objects activated the right MTG and the bilateral IPL. The latter region has been previously associated with understanding the goal of an action (e.g., Hamilton & Grafton, 2006).

Interestingly, the MTG has been also reported to be involved in the processing of functional knowledge about objects (e.g., a knife can be used for cutting; Vingerhoets, 2008; Johnson-Frey, 2004; Kellenbach, Brett, & Patterson, 2003). Therefore, it is possible that the enhanced MTG activity reflects the retrieval of stored knowledge about familiar functional object parings and their typical use (e.g., knife and fork are used for cutting), especially when interacting objects were seen from a 1PP. A match between observed (implied) action and the typical use of this object pair would facilitate understanding the goal of the observed action as suggested by the affordance-matching hypothesis (Bach et al., 2014).

However, in contrast to the AON and the MNS, viewing of paired objects did not activate IFG and PMC regions. These regions might mediate the direct matching between action observation and action execution (the mirroring mechanism; Rizzolatti et al., 2001). Converging evidence for this argument comes from Chapters 2 and 3. Both chapters found increased motor cortex activity when action-oriented objects were presented in non-standard (hand) locations for actions. The effect of hand alignment when seeing action-oriented objects seems not to infer with action intention or action goal understanding. Specifically, it is unlikely that understanding goals or intentions of others people's actions would be more difficult when observing interacting objects in non-standard relative to standard hand alignments.

Overall, the present results indicate that affordance and action understanding have distinct and shared neural representations. The concept of affordance can contribute to a better understanding of a variety of cognitive processes such as selecting objects for actions and action understanding.

7.3 Future studies

The thesis provides novel ways for studying paired-object affordance effects. Specifically, the visual search paradigm in Chapter 6, mimicking real-world scenes, encourages further investigations into the attentional capture by a tool in the presence of other objects. Previous research has indicated an automatic coupling between eye movements and upcoming actions, with eye movements preceding immediate upcoming actions by roughly half a second (Land, Mennie, & Rusted, 1999). This is in line with the observed effects of hand alignment in the action but not the colour task in Chapter 6. More precisely, the active object was prioritised when it appeared on the right side, and thus matched the preferred hand of the participants when performing the action. It would be interesting to examine whether or not the effect of tool location can be replicated with eye movement recording, or whether anticipatory glances only occur during multi-sequence actions such as tea making. Furthermore, eye tracking would help to clarify the influence of semantic distracters on affordance perception. For example, does the semantic similarity between targets and distracters evoke conflicting affordances, or do only tool-like distracters but not passive-like distracters capture attention, and thus generate a semantic interference effect?

As revealed in Chapter 2, paired-object affordance is mediated by different but interacting bilateral parieto-frontal networks. However, is it unclear how patients with parietal damage and visual extinction who behaviourally benefit from the presence of paired objects encode paired objects (Chapter 4 and 5; see also Humphreys et al., 2010a; Riddoch et al., 2006; Riddoch et al., 2003). Research in our laboratory is already under way to examine whether the same neural networks as found in healthy participants are used in extinction patients or whether additional brain areas are recruited to compensate for the lesioned brain areas. It would be expected that undamaged (left) parieto-frontal areas would be more strongly activated during observation of correctly co-located objects for action when seen from a 1PP. Further fMRI studies comparing familiar and unfamiliar object pairs would also be greatly beneficial to clarify the role of motor expertise on both the AON (e.g., Calvo-Merino et al., 2006) and on recovery from extinction (e.g., Riddoch et al., 2006).

Chapter 3 showed that the observed motor resonance was only evident in the right (non-dominant) M1. Further research should study whether the observed effects can be replicated when the MEP amplitude rather than TMS simulation intensity is kept fixed. It is plausible that the differences between left and right M1 may be more pronounced using higher TMS intensities. A future study may also wish to extend the results by manipulating the perspective in which the stimuli are presented. This would test the generalisability of the bias towards the tool. This may be particularly important for stroke rehabilitation approaches when retraining everyday tasks in patients.

Further research should also explore the reasons for the inconsistent findings of hand alignment together with the role of tools (vs. objects) within object pairs. EEG might be useful for exploring the time course and localisation of responses to object pairs aligned or not aligned with the participant’s hand. For example, if the viewing of action-related (object-tool) and tool-tool pairs (cf. Chapter 5) would elicit a similar neural response, this would confirm that the potential for action (evoked by the tool) rather than the familiarity with the action is crucial for the perception of paired-object affordance.

Another avenue for further research is to explore the possible links between action understanding (e.g., via the AON, MNS networks) and affordances. The introduction of goal manipulations to our two-item affordance displays would allow identification of shared and distinct brain areas for affordance extraction and action understanding. Furthermore, it would help to clarify the role of semantic knowledge in understanding the actions of others (Bach et al., 2014).

7.4 Conclusion

The five experiments presented in this thesis make a substantial contribution towards a better understanding of the effects of paired-object affordance on perception and attention. Firstly, they provide evidence that visual- and motor-based affordance cues contribute to the effects of paired objects. Facilitatory effects occur when visual- and motor-based affordance cues can be combined, such as seeing intact graspable, correctly co-located objects for action. Secondly, the thesis provides empirical evidence for the neural correlates of paired-object affordance. More precisely, paired-object affordance effects are mediated by different but interacting bilateral parieto-frontal networks. Thirdly, paired objects are only automatically perceived in multiple stimulus displays when the task is action-relevant (attention to objects), with the automaticity of affordance being sensitive to semantic information in the scene. The thesis also highlights which factors modulate the automaticity of affordance and further describes the interplay between attention and automaticity in the guidance of visual attention. To conclude, paired-object affordance effects are influenced by contextual information and task demands, with the active object (the tool) within a pair modulating the allocation of attention in a scene.

APPENDICES

Appendix 1: Unfamiliar object pairs used in Chapter 4

Active partner	Passive partner
Bottle opener	Paint pot
Corkscrew	Cup
Paintbrush	Potato
Peeler	Socket
Pestle	Ice cream
Plug	Mortar
Scissors	Bolt
Scoop	Wine bottle
Scourer	Plant pot
Spanner	Frying pan
Spatula	Paper
Teapot	Bottle
Tin opener	Fairy liquid
Toothbrush	Bowl
Trowel	Toothpaste
Whisk	Tin

Appendix 2: Oxford Cognitive Screen[1] test scores (Chapter 6)

Elderly participants	**Memory**			**Language**			**Praxis**	**Number**		**Attention**		
	Orientation	Verbal recall recognition	Episodic recognition	Picture naming	Sentence reading	Semantics	Imitation	Number writing	Calculation	Visual field	Broken hearts cancellation	Executive score
Cut-off score	*less than 4*	*less than 3*	*less than 3*	*less than 3*	*less than 14*	*less than 3*	*less than 8*	*less than 3*	*less than 3*	*less than 4*	*less than 42*	*greater than ± 4*
E16	4	4	4	4	15	3	10	3	4	4	**31**	0
E17	4	4	4	4	15	3	11	3	3	4	47	3
E18	4	4	4	3	15	3	12	3	4	4	50	-1
E19	4	4	4	4	15	3	11	3	**2**	4	48	-1
E20	4	4	4	4	15	3	12	3	4	4	50	-1
E21	4	4	4	4	15	3	12	3	4	4	49	-1
E22	No data obtained											
E23	4	4	3	4	15	3	12	3	4	4	48	-1
E24	4	4	4	4	15	3	12	3	4	4	49	**-4**
E25	4	4	4	4	15	3	12	3	4	4	50	-1
E26	4	4	4	4	15	3	10	3	4	4	49	-1
E27	4	4	4	4	15	3	12	3	4	4	50	-1
E28	4	4	3	4	15	3	12	3	4	4	50	**5**
E29	4	4	4	3	15	3	11	3	4	4	50	-1
E30	4	4	4	4	15	3	11	3	4	4	50	-1

Note. Impaired performance is highlighted in bold.

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[1] Demeyere, N., Riddoch, M. J., Slavkova, E. D., Bickerton, W. L., & Humphreys, G. W. (2015). The Oxford Cognitive Screen (OCS): Validation of a Stroke-Specific Short Cognitive Screening Tool. *Psychological Assessment*.

Appendix 3: ANOVA summary for the accuracy data when only one run of each participant was analysed (224 trials; Chapter 6)

Effect	F	p	η_p^2
Task	*F*(1, 40) = 3.833	.057	.087
Distracter	*F*(1, 40) = 30.288	.000	.431
Congruence	*F*(1, 40) = 47.878	.000	.545
Age	*F*(2, 40) = 3.953	.027	.165
Task x Distracter	*F*(2, 40) = 124.242	.000	.756
Distracter x Congruence	*F*(2, 40) = 2.052	.030	.112
Task x Congruence	*F*(2, 40) = .061	.806	.002
Task x Age	*F*(2, 40) = 6.189	.005	.236
Distracter x Age	*F*(2, 40) = 4.613	.016	.187
Congruence x Age	*F*(2, 40) = 2.715	.078	.120
Task x Distracter x Congruence	*F*(2, 40) = 37.570	.000	.484
Task x Distracter x Congruence x Age	*F*(2, 40) = 1.337	.274	.063

Appendix 4: Accuracy and standardised reaction time (RT) data (Chapter 6)

Task	Distracter	Congruence	Side Active Object	Accuracy			zRT		
				Young	Middle-aged	Elders	Young	Middle-aged	Elders
Action	Related	Congruent	Left	0.93 (0.26)	0.98 (0.13)	0.96 (0.20)	0.38 (1.06)	0.44 (0.96)	0.33 (1.15)
			Right	0.93 (0.26)	0.97 (0.17)	0.94 (0.24)	0.38 (0.97)	0.39 (1.05)	0.28 (0.92)
		Incongruent	Left	0.94 (0.24)	0.98 (0.13)	0.91 (0.28)	0.47 (1.07)	0.59 (0.99)	0.34 (1.04)
			Right	0.86 (0.35)	0.91 (0.28)	0.89 (0.32)	0.52 (0.94)	0.46 (1.02)	0.43 (1.04)
	Unrelated	Congruent	Left	0.93 (0.25)	0.98 (0.13)	0.95 (0.23)	0.37 (0.99)	0.52 (1.06)	0.36 (0.91)
			Right	0.94 (0.24)	0.99 (0.07)	0.94 (0.24)	0.34 (1.04)	0.45 (1.09)	0.22 (0.81)
		Incongruent	Left	0.93 (0.25)	0.99 (0.10)	0.91 (0.28)	0.57 (0.94)	0.65 (1.08)	0.42 (1.11)
			Right	0.92 (0.27)	0.98 (0.12)	0.92 (0.27)	0.53 (1.09)	0.55 (1.02)	0.35 (1.13)
Colour	Related	Congruent	Left	0.97 (0.17)	0.95 (0.22)	0.97 (0.16)	-0.53 (0.51)	-0.51 (0.56)	-0.41 (0.61)
			Right	0.96 (0.20)	0.99 (0.10)	0.97 (0.17)	-0.49 (0.45)	-0.54 (0.47)	-0.44 (0.53)
		Incongruent	Left	0.96 (0.20)	0.98 (0.13)	0.98 (0.14)	-0.53 (0.46)	-0.52 (0.62)	-0.41 (0.57)
			Right	0.96 (0.19)	0.98 (0.13)	0.99 (0.11)	-0.48 (0.49)	-0.54 (0.53)	-0.48 (0.44)
	Unrelated	Congruent	Left	0.97 (0.17)	0.99 (0.11)	0.97 (0.17)	-0.58 (0.46)	-0.59 (0.53)	-0.53 (0.49)
			Right	0.91 (0.29)	0.92 (0.28)	0.92 (0.28)	-0.59 (0.45)	-0.52 (0.52)	-0.43 (0.68)
		Incongruent	Left	0.92 (0.28)	0.93 (0.25)	0.93 (0.26)	-0.48 (0.54)	-0.51 (0.53)	-0.49 (0.49)
			Right	0.86 (0.35)	0.87 (0.34)	0.86 (0.36)	-0.51 (0.49)	-0.49 (0.62)	-0.37 (0.58)

Note. zRT = Normalised reaction time. Standard deviation in brackets.

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Endnote

[i] All patients were also impaired on a short computer-based test of visual extinction, defining their inclusion in the study. In this test, we presented the letters A to D, 0.5° x 0.5° centred at locations 3° to the left or right side of fixation. The letters were presented for 200 ms unmasked either alone (randomly in the left or right field) or bilaterally. Patients had to identify the letters presented. There were 24 single left trials, 24 single right and 48 two-item trials. Patients were classified as having extinction if they showed a lateralised difference of more than 2 when reporting items under bilateral relative to unilateral conditions. A group of 12 age-matched control patients were able to report all the items under these presentation conditions. All the patients met this definition for extinction.